

EVOLUTION OF SEED SIZE, SHAPE, AND SURFACE ARCHITECTURE IN THE TRIBE EPILOBIEAE (ONAGRACEAE)¹

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ABSTRACT

The seeds of more than half of the approximately 210 species of Onagraceae tribe Epilobieae were examined with the scanning electron microscope. The six species of *Boisduvalia* have irregularly angular-fusiform seeds with convex, flat, irregularly polygonal surface cells in two species and an irregularly striated reticulum formed by the unevenly joining walls of the surface cells in the four others. They are similar to one another and sharply distinct from those of *Epilobium*, although the relationship between the genera is undoubtedly close. The seeds of *Epilobium* fall in seven groups: (1) large, obovoid seeds with a more or less prominent micropylar constriction, in three small sections of generalized xerophytes and in one species, *E. rigidum*, of sect. *Epilobium*; (2) smaller papillose seeds in over half of the other species; (3) foveolate seeds, independently evolved in many species; (4) obovoid-patelliform seeds in four Australasian species; (5) irregularly reticulate seeds in one subsection of *Epilobium* sect. *Chamaenerion*; (6) ridged seeds in a phylogenetically coherent group of North American origin; (7) finely papillose, distinctive seeds in sect. *Crossostigma*. More or less prominent chalazal beaks have evolved in some species. From xerophytic ancestors, *Epilobium* has evolved a highly successful group of mesophytes in sect. *Epilobium* that have achieved worldwide distribution. This trend seems to have been accompanied by an increase in seed number and a concomitant decrease in seed size.

The well-marked tribe Epilobieae, one of six that make up the family Onagraceae, includes some 200 species of *Epilobium*, of worldwide distribution; and six of *Boisduvalia*, five of western North America, with one common to Argentina, and one additional species restricted to western South America. The western North American *Zauschneria*, often recognized as distinct from *Epilobium*, is based on a red-flowered, bird-pollinated species of one of the constituent groups of *Epilobium*. *Zauschneria* has accordingly been reduced to the status of a section of *Epilobium* (Raven, 1976). Of the six sections of *Epilobium*, two, with a total of three species, consist of annuals and are restricted to western North America; two others, with a total of four species, are generalized xerophytic perennials of western North America; one, *Chamaenerion*, includes seven species of Eurasia, two of which extend to North America; and the remaining one, sect. *Epilobium*, consists of some 185 species, found on every continent except Antarctica, but especially well represented at high altitudes and high latitudes.

The surface sculpturing of the seeds of *Epilobium* has long been employed as an important taxonomic character (cf. Haussknecht, 1884; Samuelsson, 1923,

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1930; Munz, 1965), and it is natural that these seeds have been investigated in recent years with the scanning electron microscope (SEM). The regional or more limited studies that have been concerned with the scanning electron microscopy of the seeds of *Epilobium* are the following: Berggren (1974), Denford & Karas (1974), Skvortsov & Rusanovitch (1973, 1974), Raven & Raven (1976), and Seavey et al. (1977). To a certain extent, these studies have provided background for the present more comprehensive effort.

In addition to the surface variations seen with the SEM, seeds of Epilobieae vary considerably in size and shape. It is the purpose of our report to evaluate these seed characters against a background of other lines of systematic investigation, including cytology, morphology, and biogeography. Included in this analysis are more than half of the approximately 210 species of Epilobieae, representing the entire range of diversity; four of the seven species of sect. *Chamaenerion*; and all species of the remaining sections of *Epilobium*, as well as all six species of *Boisduvalia*.

The seeds of all but one of the species of *Epilobium* possess a tuft of trichomes, the coma, on their chalazal (distal) end, whereas none of the species of *Boisduvalia* have a coma. Although some variation exists in the color and relative strength of attachment of the coma (cf. Raven & Raven, 1976), no differences in its ultrastructure have been detected and this feature of seed anatomy is not dealt with in the present report.

MATERIALS AND METHODS

Seeds were collected from recently grown garden plants or from herbarium sheets. The coma was removed in most cases, but left intact if removal damaged the chalazal end of the seed. The seeds were then mounted on aluminum stubs with double-sticky tape, coated with gold/platinum in a Technics Hummer I and examined with a Cambridge Stereoscan Mark 2A scanning electron microscope, operated at an accelerating voltage of 20KV, at the Department of Pathology, Medical School, Washington University. About 75 other samples were photographed in the same way in the Electron Microscope Section of the Physics and Engineering Laboratory, D.S.I.R., Lower Hutt, New Zealand, and the results of examining these photographs are likewise incorporated into the present paper.

Four to six seeds of each sample were mounted and inspected. Little variation within samples was evident, and the seed photographed was in all cases judged to be typical for the sample. Photographs were taken at approximately 60 $\times$, 240 $\times$, and 1200 $\times$. The higher magnification photographs were taken near the center of the seed, but since little variation is usually evident over the surface of this seed, this practice was not strictly followed in all cases.

A list of specimens from which seeds were taken for the illustrations (Figs. 1–210) in this paper is presented in Table 1. Voucher numbers are given in the legends of Figs. 1–210 only when more than one collection is listed in Table 1. Bars at the top of each plate indicate, respectively, 0.5 mm, 125 μ m, and 25 μ m.

TABLE 1. Voucher information for species of *Boisduvalia* and *Epilobium* illustrated in this paper. *M* and *G* numbers refer to garden planting numbers, used also on herbarium vouchers; *R* numbers are *Raven* collections. All vouchers are deposited at the Missouri Botanical Garden (MO), unless otherwise indicated.

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- Boisduvalia cleistogama* Curran. U.S.A., Calif., Yolo Co., *Crampton* 9222.
- B. densiflora* (Lindl.) S. Wats. U.S.A., Calif., Fresno Co., near Auberry, *Seavey* in 1974, *M130*.
- B. glabella* (Nutt.) Walp. U.S.A., Calif., Solano Co., near Elmira, *Crampton* 9219.
- B. macrantha* Heller. U.S.A., Calif., Modoc Co., near Lookout, *Seavey* in 1974, *M137*.
- B. stricta* (A. Gray) Greene. U.S.A., Calif., Fresno Co., near Auberry, *Seavey* in 1974, *M133*.
- B. subulata* (Ruiz & Pavón) Raimann. Chile, Ñuble, *Cheese & Watson* 4405, *M158*.
- Epilobium alpestre* (Jacq.) Krock. Switzerland, Canton Vaud, seed from Conservatoire et Jardin botaniques, Genève, 1972–1788, *M31*.
- E. alsinifolium* Vill. U.S.S.R., Transcarpathia, *Skvortsov* in 1968 (DS), *R26179*.
- E. amurense* Hausskn. Japan, Pref. Yamanashi, Hayakawa-cho, *Deguchi* in 1974, *M80*.
- E. anagallidifolium* Lam. U.S.S.R., E. Chukotka, Iskaten Range, *Kozhevnikov* in 1972, *M718*.
- E. angustifolium* L. subsp. *circumvagum* Mosquin. U.S.A., Calif., Onion Valley, *Twisselmann* 5825 (CAS).
- E. atlanticum* Litard. & Maire. Spain, Sierra Nevada, *R26166*.
- E. behringianum* Hausskn. Alaska, Kiska Quad., Buldir Is., *Dick* 414, *M294*.
- E. billardierianum* Sér. subsp. *billardierianum*. New Zealand, Nelson, *Brockie* CHR199322, *M4*.
- E. canum* (Greene) Raven subsp. *garrettii* (A. Nels.) Raven. U.S.A., Utah, Washington Co., Zion Natl. Park, *Seavey* in 1974, *G865*.
- E. canum* subsp. *canum*. U.S.A., Calif., Santa Barbara Co., Santa Cruz Is., seed from Rancho Santa Ana Botanic Garden, *G844*.
- E. canum* subsp. *septentrionale* (Keck) Raven. U.S.A., Calif., Humboldt Co., Trinity River, *Tracy* 5974.
- E. canum* subsp. *latifolium* (Keck) Raven. U.S.A., Calif., Lake Co., Snow Mt., *Seavey* in 1974, *G807*.
- E. chilense* Hausskn. Chile, Prov. Cautín, near Lake Icalma, *Zöllner* 7868, *M108*.
- E. ciliatum* Raf. U.S.A., Oregon, Josephine Co., near O'Brien, *Seavey* 1119.
- E. coloratum* Biehler. Seeds from Copenhagen Botanical Gardens, *M88*.
- E. davuricum* Fisch. Canada, Yukon Terr., *Porsild* 306 (UBC); U.S.S.R., S.E. Chukchi Peninsula, *Yurtsev & Raszhivin* in 1972.
- E. denticulatum* Ruiz & Pavón. Peru, Pampa to Yamobamba, ca. 70 km E. of Trujillo, *Conrad* 2715, *M83*.
- E. dodonaei* Vill. U.S.S.R., no voucher.
- E. duriae* Gay ex Godron. Spain, Puerto Ventana, Oviedo, *Merxmüller & Grau* 21360, *R26258*.
- E. exaltatum* Drew. U.S.A., Calif., Siskiyou Co., *Seavey* in 1971, *M409*; Washington, Clallam Co., *Seavey* 1111, *M559*.
- E. fauriei* H. Lév. Japan, Tottori Pref., *Yamamoto* in 1970, *M265*.
- E. foliosum* (Nutt. ex Torr. & A. Gray) Suksd. U.S.A., Oregon, Douglas Co., *Raven* 19089.
- E. glaucum* Phil. Chile, Prov. Curicó, Dept. Curicó, *Martcorena, Matthei & Rodríguez* 1, *M68*.
- E. gunnianum* Hausskn. Australia, N.S.W., New England Natl. Park, *Raven & Englehorn* 25853.
- E. hirsutum* L. U.S.S.R., E. Kazakhstan, Altai Mts., *Belianina* in 1969 (DS), *M58*.
- E. hirtum* Samuelsson. Peru, 20 km W. of Arequipa, *Averett* 1004, *M341*.
- E. hornemannii* Reichenb. s. lat. U.S.S.R., E. Chukchi Peninsula, *Yurtsev & Sytin* in 1971.
- E. komarovianum* H. Lév. New Zealand, near Mt. Cook, *Raven & Englehorn*. CHR-199430 (MO).
- E. latifolium* L. U.S.S.R., Dist. Barguzin, *Makeeva* in 1971.
- E. leiophyllum* Hausskn. Afghanistan, S. of Unai Pass, *Breckle* A2717, *G352*.
- E. luteum* Pursh. Alaska, Juneau, *Shumway* in 1891 (GH).
- E. minutum* Lindl. ex Lehm. U.S.A., Calif., Plumas Co., *Howell* 51156.
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TABLE 1. (continued)

<i>E. nesophilum</i> Fern. Canada, St. Phillips, Newfoundland, <i>Olsen in 1974, M121.</i>
<i>E. nevadense</i> Munz. U.S.A., Nevada, Clark Co., Charleston Mts., <i>Seavey in 1974, G808.</i>
<i>E. nivium</i> T.S. Brandege. U.S.A., Calif., Lake Co., Snow Mts., <i>Seavey in 1974, G866.</i>
<i>E. nutans</i> Schmidt. Czechoslovakia, W. Bohemia, <i>Kral in 1967, G23.</i>
<i>E. obcordatum</i> A. Gray subsp. <i>obcordatum</i> . U.S.A., Calif., Mono Co., Oneida Lake, <i>Mc-Millan 59-1 (CAS).</i>
<i>E. obcordatum</i> subsp. <i>siskiyouense</i> Munz. U.S.A., Calif., Siskiyou Co., Sacramento River headwaters, <i>Pringle 1882 (NY).</i>
<i>E. obscurum</i> Schreb. England, Surrey, <i>Raven 26092, M2.</i>
<i>E. oreganum</i> Greene. U.S.A., Oregon, Josephine Co., near O'Brien, <i>Seavey 1117.</i>
<i>E. oregonense</i> Hausskn. U.S.A., Calif., Mono Co., Rock Creek, <i>Seavey in 1970, G350.</i>
<i>E. palustre</i> L. U.S.S.R., Chukchi Peninsula, <i>Yurtsev & Raszhivin in 1972.</i>
<i>E. paniculatum</i> Nutt. ex Torr. & A. Gray. U.S.A., Oregon, Josephine Co., near O'Brien, <i>Seavey in 1975, M554.</i>
<i>E. cf. pauciflorum</i> Samuelsson. Chile, on the pass of Lolco, <i>Zöllner 6245, M110.</i>
<i>E. pictum</i> Petrie. New Zealand, Tasman Valley, <i>Raven & Wilson 25617.</i>
<i>E. platystigmatosum</i> C. B. Robinson. Taiwan, Hualien Co., <i>K. S. Hsu 1714, G657.</i>
<i>E. pylaeanum</i> Fern. Canada, Newfoundland, St. Stephen's, <i>Olsen in 1974, M127.</i>
<i>E. pyrricholophum</i> Fr. & Sav. Japan, Nikko, seeds from University of Tokyo Botanical Garden, <i>Tochi, M73.</i>
<i>E. rigidum</i> Hausskn. U.S.A., Oregon, Josephine Co., <i>Seavey 1116</i> ; Calif., Del Norte Co., <i>Curtis 1 (RSA).</i>
<i>E. scalare</i> Fern. Canada, Newfoundland, Highlands of St. John, <i>Fernald & Long 28728 (GH).</i>
<i>E. shiromense</i> Matsum. & Nakai. Japan, Pref. Yamanashi, <i>Deguchi in 1974, M81.</i>
<i>E. stereophyllum</i> Fresen. Kenya, Aberdare Natl. Park, <i>Raven 26164, M78.</i>
<i>E. stevenii</i> Boiss. Iran, Azerbaijan Prov., <i>Termé in 1971.</i>
<i>E. strictum</i> Muhl. Canada, Ottawa, Ontario, Carleton Co., <i>Frankton in 1974, M65.</i>
<i>E. suffruticosum</i> Nutt. U.S.A., Wyoming, Teton Co., Teton Natl. Park, <i>Raven 26464.</i>
<i>E. treleasianum</i> H. Lév. British Columbia, near Bouff, <i>Price 1900 (GH).</i>
<i>E. sp.</i> Argentina, Estancia Moat, Tierra del Fuego, <i>Moore 1686, M254</i> ; like <i>E. cunninghamii</i> Hausskn. except for pubescence.

OBSERVATIONS

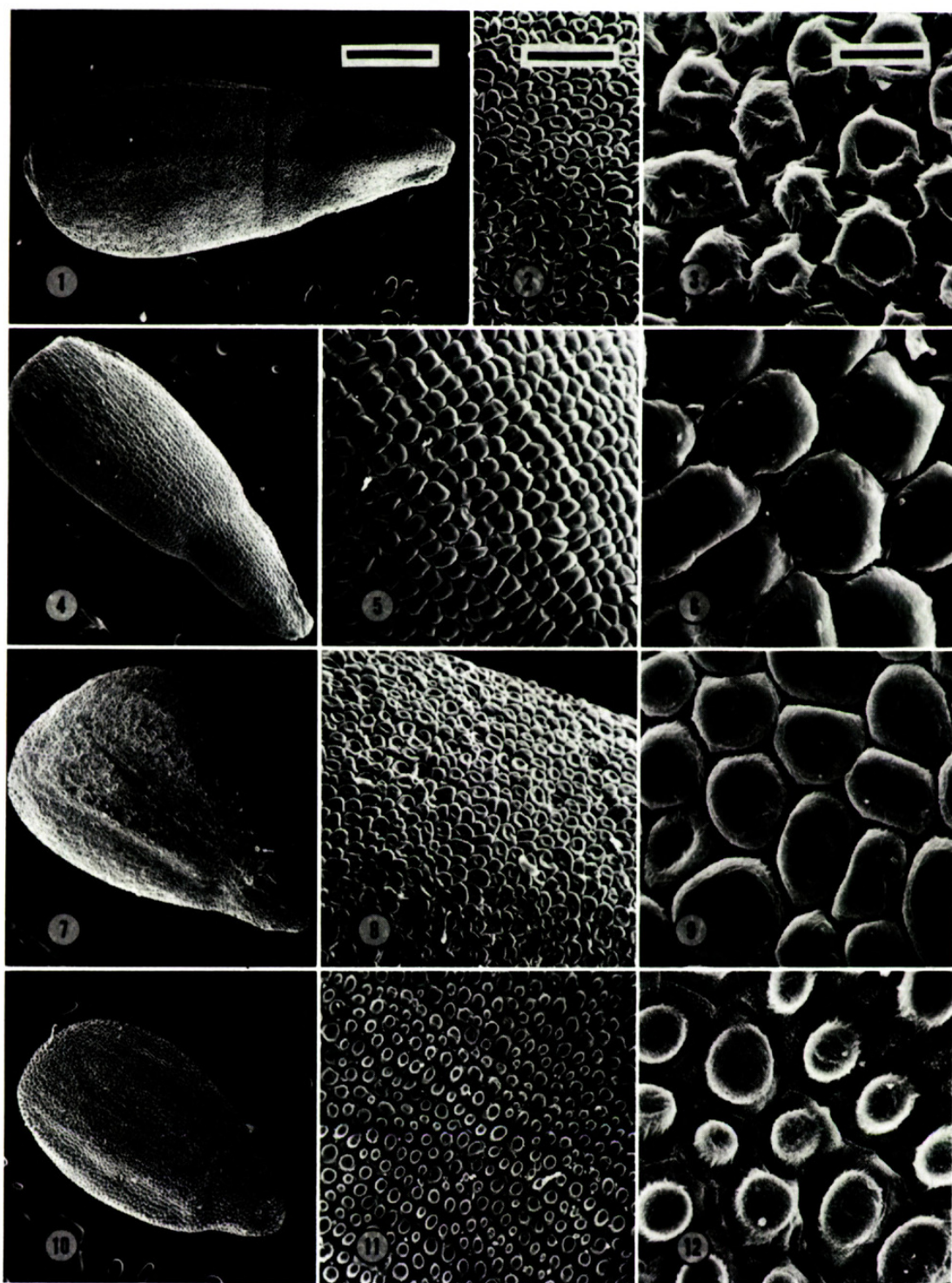
I. *Epilobium*

The results are presented according to the sections recognized by Raven (1976).

Sect. *Cordylophorum* (3 species):

Epilobium nevadense (Figs. 1-3), *E. nivium* (Figs. 7-9), and *E. suffruticosum* (Figs. 4-6), all have relatively large seeds (2.0-2.7 mm) with a prominent constriction toward the micropylar end. The seeds of *E. nevadense* are obovoid, those of *E. suffruticosum* clavate, and those of *E. nivium* broadly obovoid. The cells at the point of attachment of the coma form a distinct, although small, neck region at the chalazal end.

The surface cells of *E. nevadense* (Fig. 3) are unique in shape. The center of each cell is occupied by a thick, crater-shaped, apparently collapsed tangential wall. The surface cells of the two other species are entirely convex, giving a cobblestone appearance at high magnification (Figs. 6, 9). With respect to seed characters, *E. suffruticosum* resembles *E. nevadense* more than either resembles *E. nivium*.



FIGURES 1-12. Scanning electron micrographs of seeds of *Epilobium*, sects. *Cordyllophorum* and *Xerolobium*.—1-3. *E. nevadense* (*Cordyllophorum*).—4-6. *E. suffruticosum* (*Cordyllophorum*).—7-9. *E. nivium* (*Cordyllophorum*).—10-12. *E. paniculatum* (*Xerolobium*).

Sect. *Xerolobium* (1 species):

The large, broadly obovoid seeds of *E. paniculatum* (Figs. 10–12) also have a prominent constriction toward the micropylar end. The tangential walls of the surface cells have a centrally situated convex prominence (Fig. 12). The seeds of this species are similar to those of *E. nivium*. The neck region is inconspicuous.

Sect. *Zauschneria* (1 species):

The seeds of four of the six subspecies of *Epilobium canum* are presented in Figs. 13–24. Resembling those of the preceding section, these seeds are large and broadly obovoid; and, like all of the species of the preceding two sections, they have a constriction toward the micropylar end. The neck region is inconspicuous, but, as in those of the preceding sections, distinct, especially when viewed from a low angle (e.g., *E. canum* subsp. *canum*, Fig. 199). The tangential walls of the surface cells are entirely convex with little radial wall evident, except for subsp. *canum* (Figs. 16–18), in which the tangential walls are convex but sunken within prominent radial walls.

Sect. *Chamaenerion* (7 species):

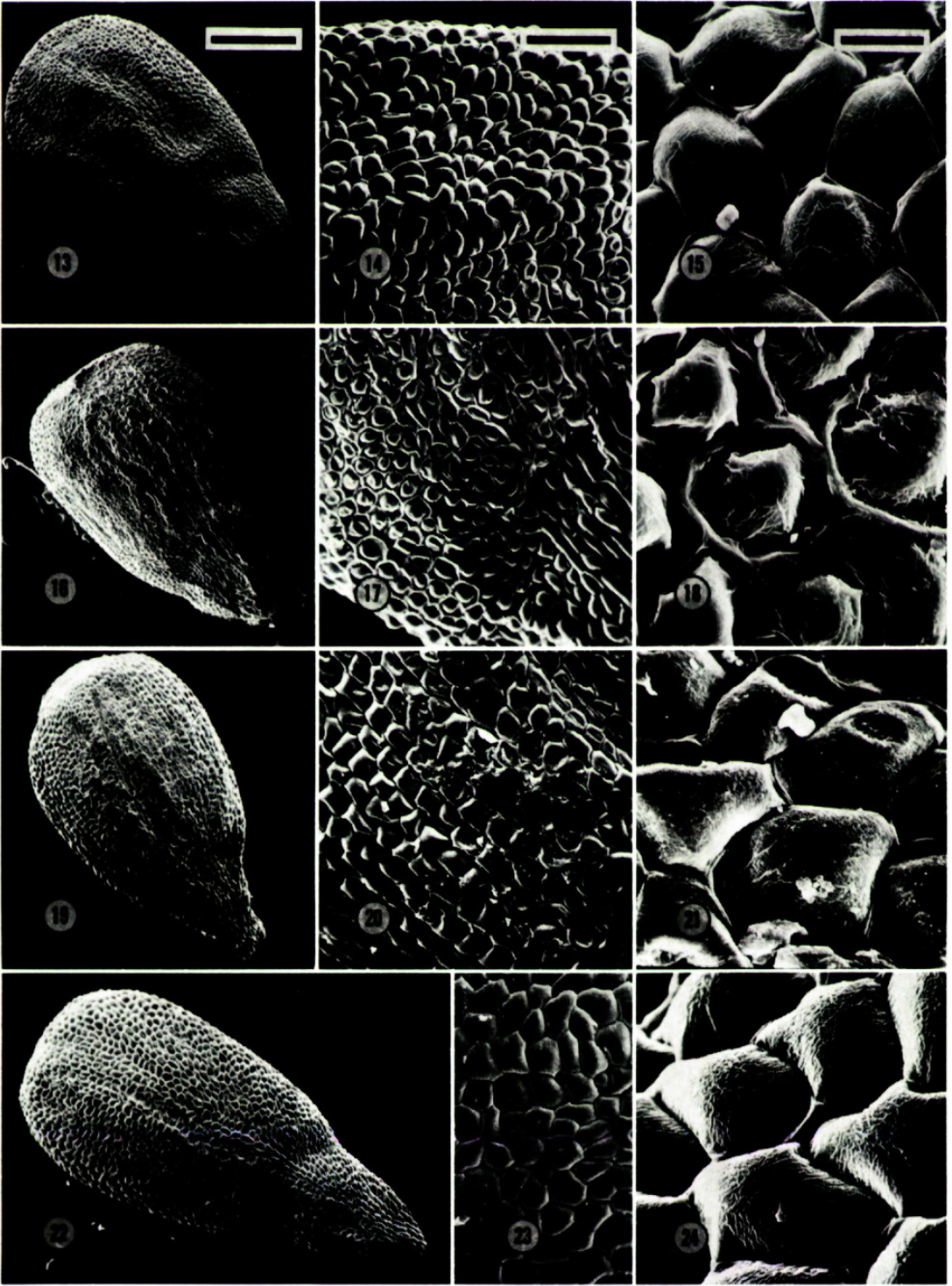
The seeds of this section are small (1.0–1.8 mm) and relatively narrower than those of the preceding three sections (Figs. 25–36). The neck region is evident in dorsal view and is composed of irregularly constricted chalazal end cells (e.g., *E. latifolium*, Fig. 209). The surface cells of the three species of subsect. *Leiostylae*, *E. angustifolium* (Figs. 25–27), *E. conspernum* Hausskn., and *E. latifolium* (Figs. 28–30), lack convex tangential walls, and the major feature of the surface is the irregularly polygonal reticulum formed by the radial walls (Figs. 27, 30). The two species of subsect. *Rosmarinifolium* we examined, *E. stevenii* (Figs. 31–33) and *E. dodonaei* (Figs. 34–36) are of approximately the same size and shape, but the surface tangential walls appear as raised, irregularly compressed areas in the center of prominent regularly polygonal radial walls.

Sect. *Crossostigma* (2 species):

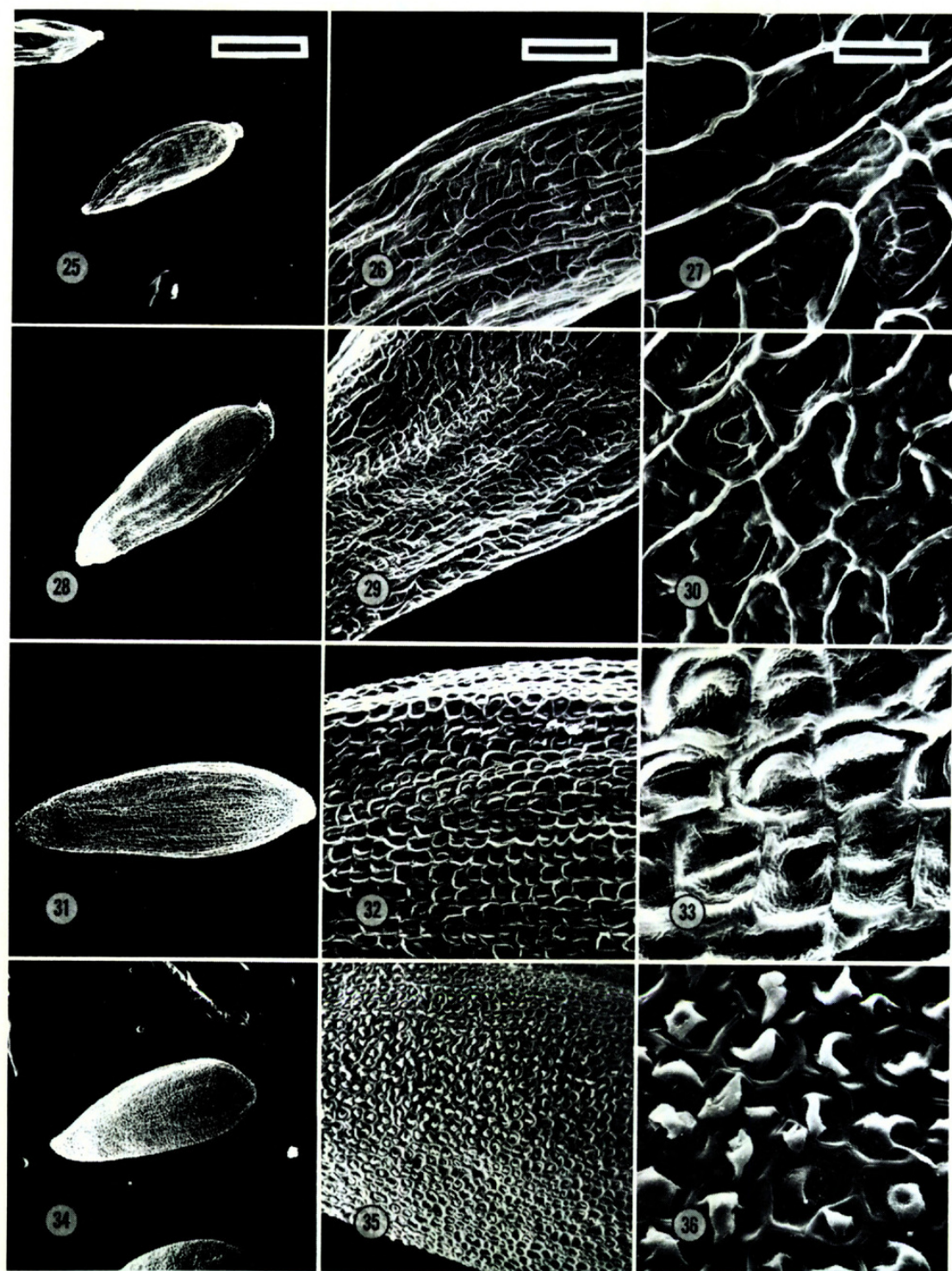
These small, obovoid seeds, blunt at both ends, are unique in the tribe in their very finely papillose surface cells (Seavey et al., 1977). The surface cells of *E. minutum* (Figs. 193–195) are concave and very finely papillose over the tangential walls as well as the prominent reticulate radial walls (Fig. 195), whereas the surface in *E. foliosum* (Figs. 196–198) has isolated convex, smooth tangential walls surrounded by finely papillose, elevated radial walls. The neck region in both species is inconspicuous.

Sect. *Epilobium* (ca. 185 species):

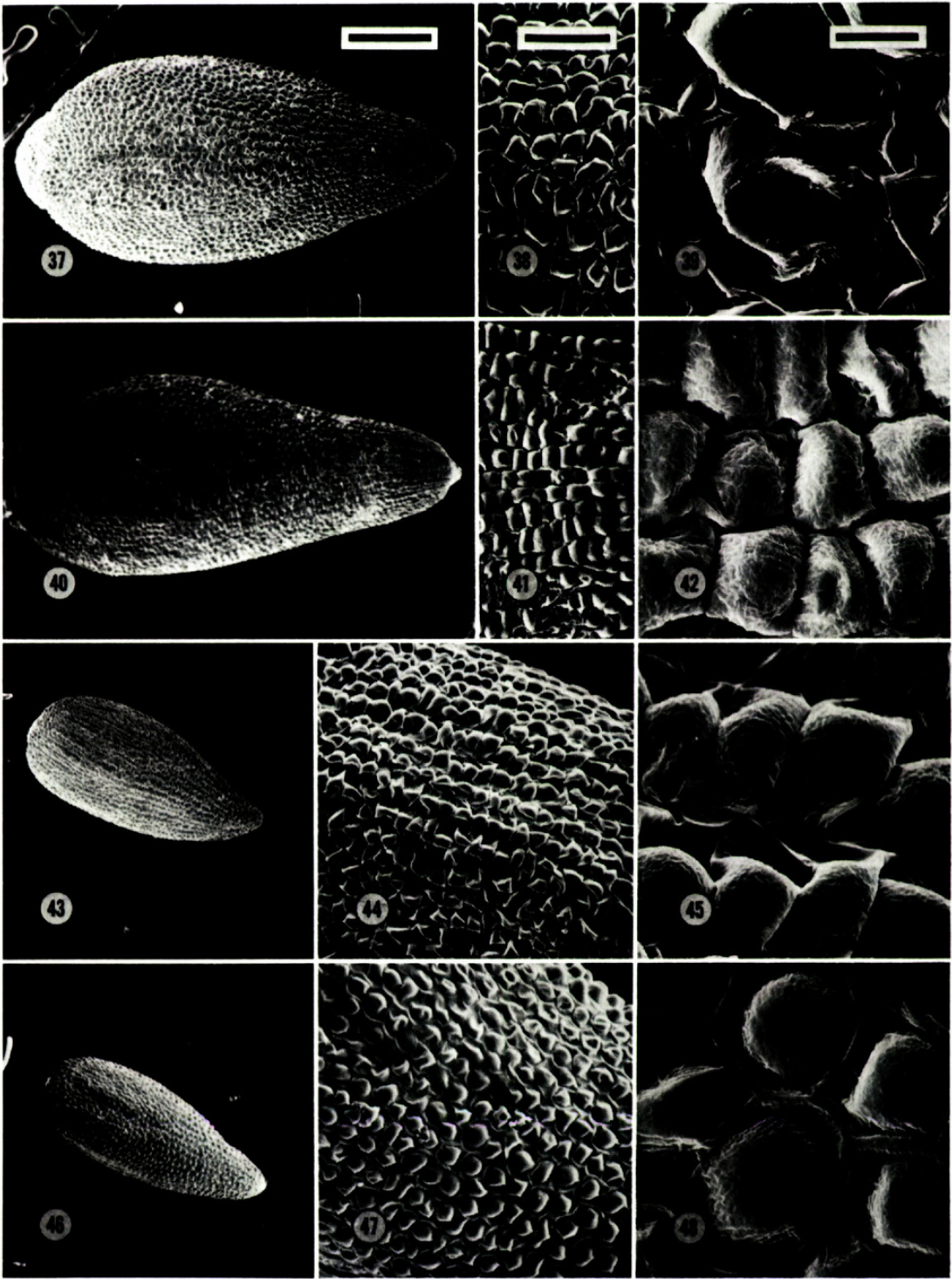
Extensive variation exists in the size, shape, and surface architecture of the species of this large section. Representatives of the species with the largest seeds, *E. rigidum* (Figs. 37–39, 40–42), may possess a prominent (Fig. 37) or relatively obscure (Fig. 40) constriction toward the micropylar end, resembling those of sect. *Cordylophorum*. The surface cells of this species are convex over most of their surface, and the radial walls are mostly obscured (Figs. 39, 42).



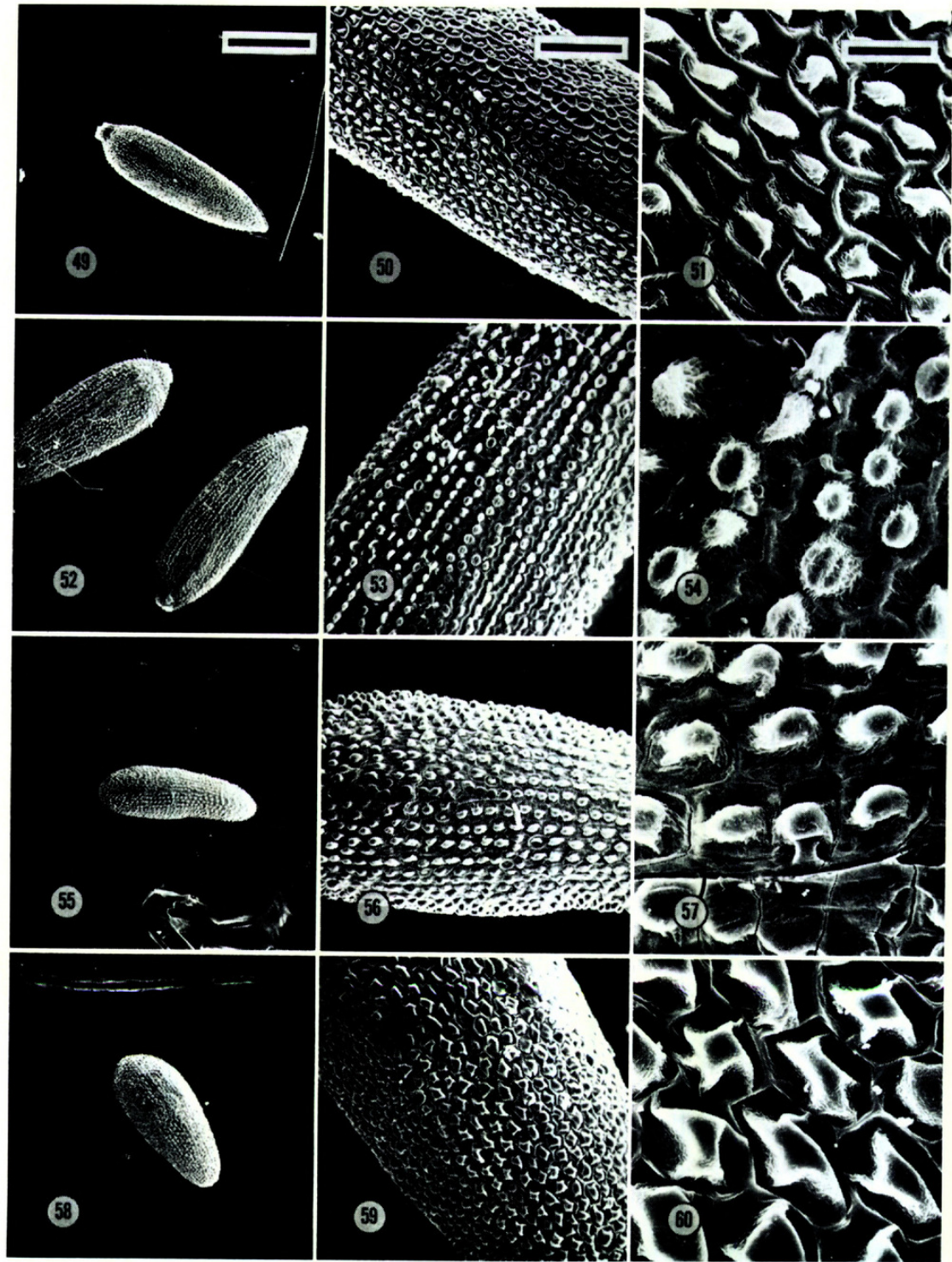
FIGURES 13–24. Scanning electron micrographs of seeds of *Epilobium* sect. *Zauschneria*.—13–15. *E. canum* subsp. *garrettii*.—16–18. *E. canum* subsp. *canum*.—19–21. *E. canum* subsp. *septentrionale*.—22–24. *E. canum* subsp. *latifolium*.



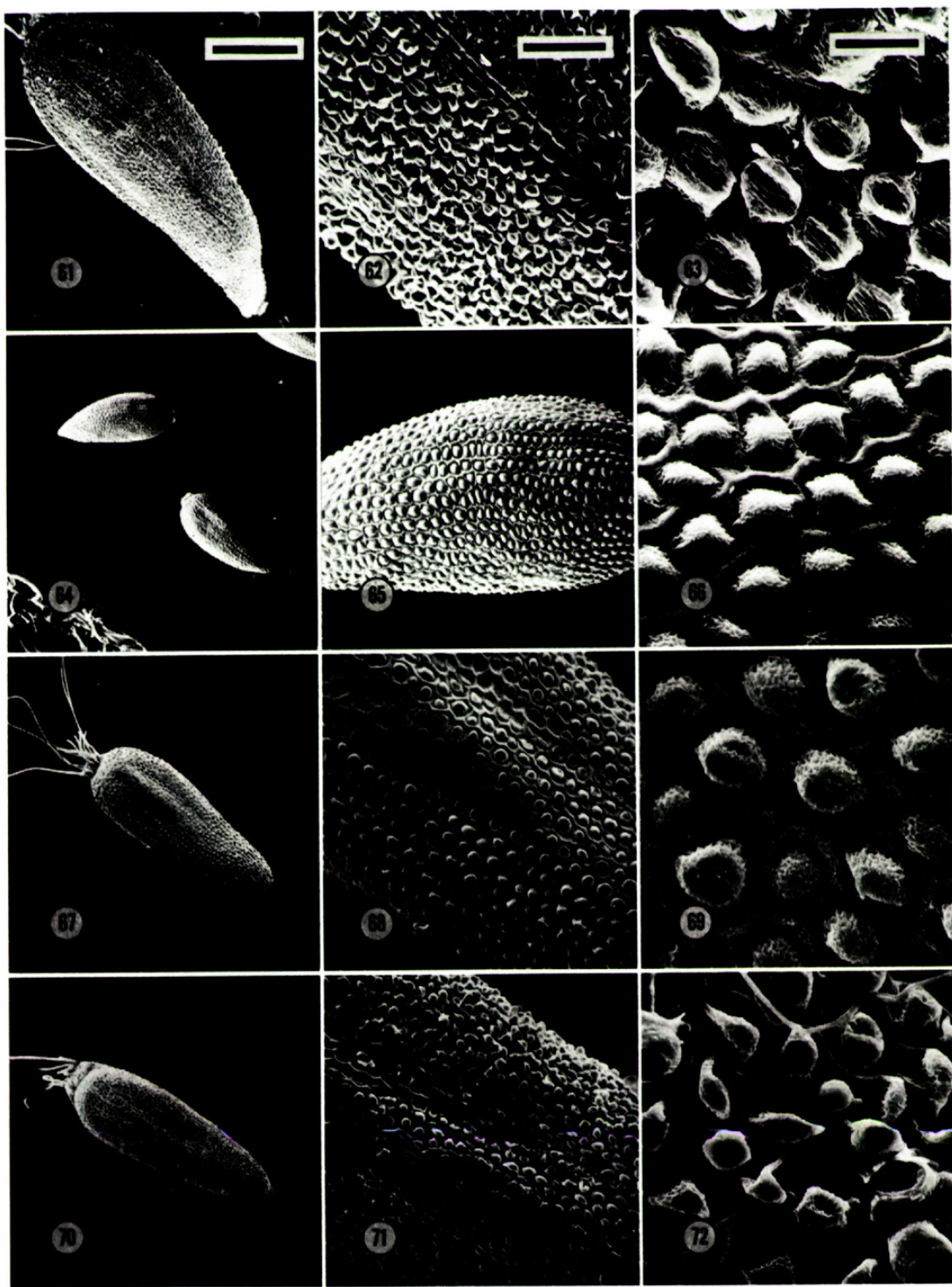
FIGURES 25–36. Scanning electron micrographs of seeds of *Epilobium* sect. *Chamaenerion*.—25–27. *E. angustifolium*.—28–30. *E. latifolium*.—31–33. *E. stevenii*.—34–36. *E. dodonaei*. The first two species belong to subsect. *Leiostylae*, the second two to subsect. *Rosmarinifolium*.



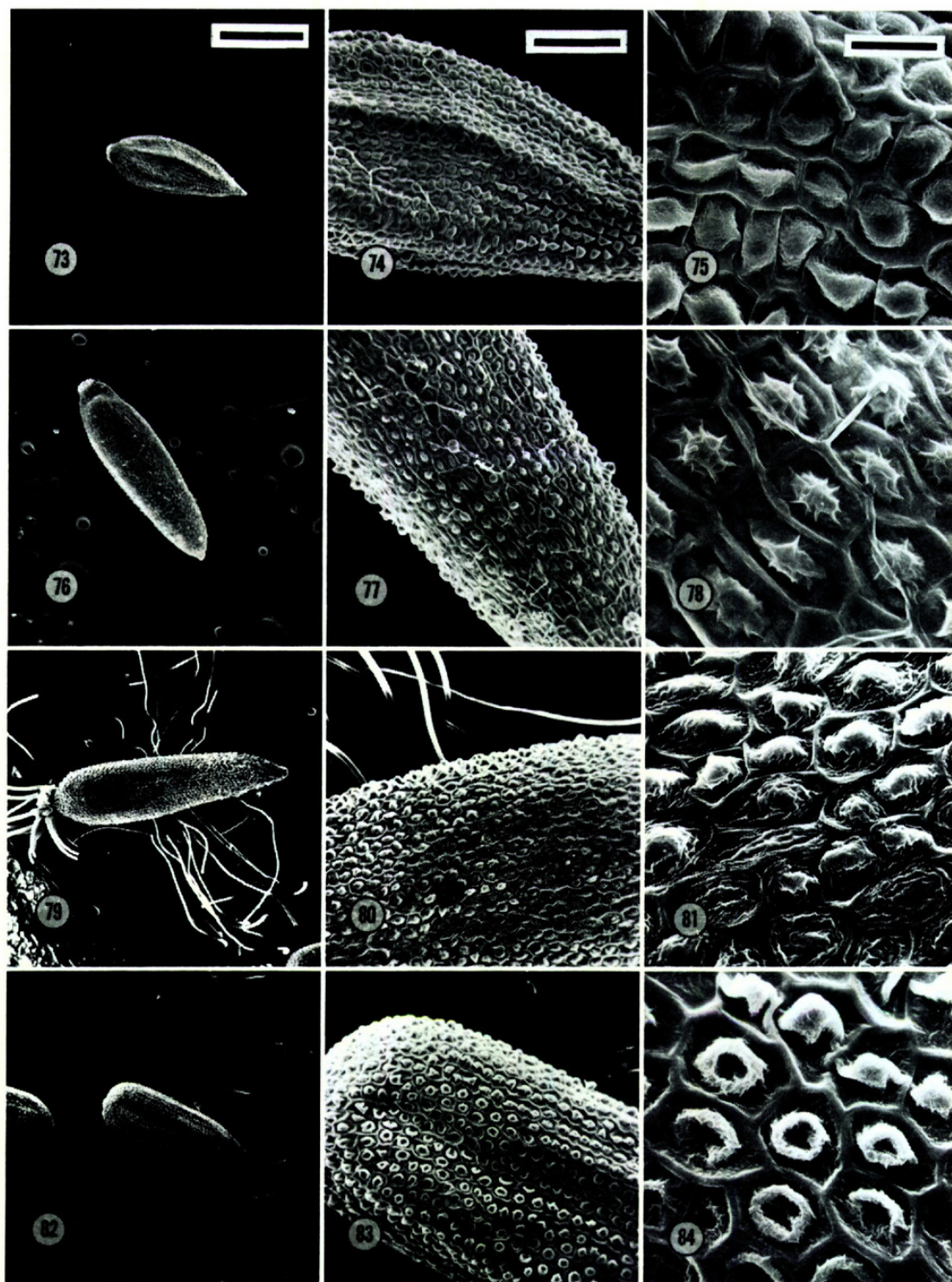
FIGURES 37–48. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—37–39. *E. rigidum*, Seavey 1116.—40–42. *E. rigidum*, Curtis 1.—43–45. *E. obcordatum* subsp. *obcordatum*.—46–48. *E. obcordatum* subsp. *siskiyouense*.



FIGURES 49–60. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—49–51. *E. shiroumense*.—52–54. *E. fauriei*.—55–57. *E. platystigmatosum*.—58–60. *E. stereophyllum*.



FIGURES 61-72. Scanning electron micrographs of South American species of *Epilobium* sect. *Epilobium*.—61-63. *E. cf. pauciflorum*.—64-66. *E. denticulatum*.—67-69. *E. glaucum*.—70-72. *E. sp.*



FIGURES 73–84. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—73–75. *E. hirtum*.—76–78. *E. oregonense*.—79–81. *E. coloratum*.—82–84. *E. leiophyllum*.

This combination of characters is unique in sect. *Epilobium*. The seeds of *E. obcordatum* (Figs. 43–45, 46–48) are similar in surface relief (esp. Fig. 45), but they are smaller and lack a prominent constriction at the micropylar end.

The remaining species of sect. *Epilobium* have seeds which are smaller, lack

a micropylar constriction, and are characterized by surface cells which, although often convex, always have clearly evident radial walls.

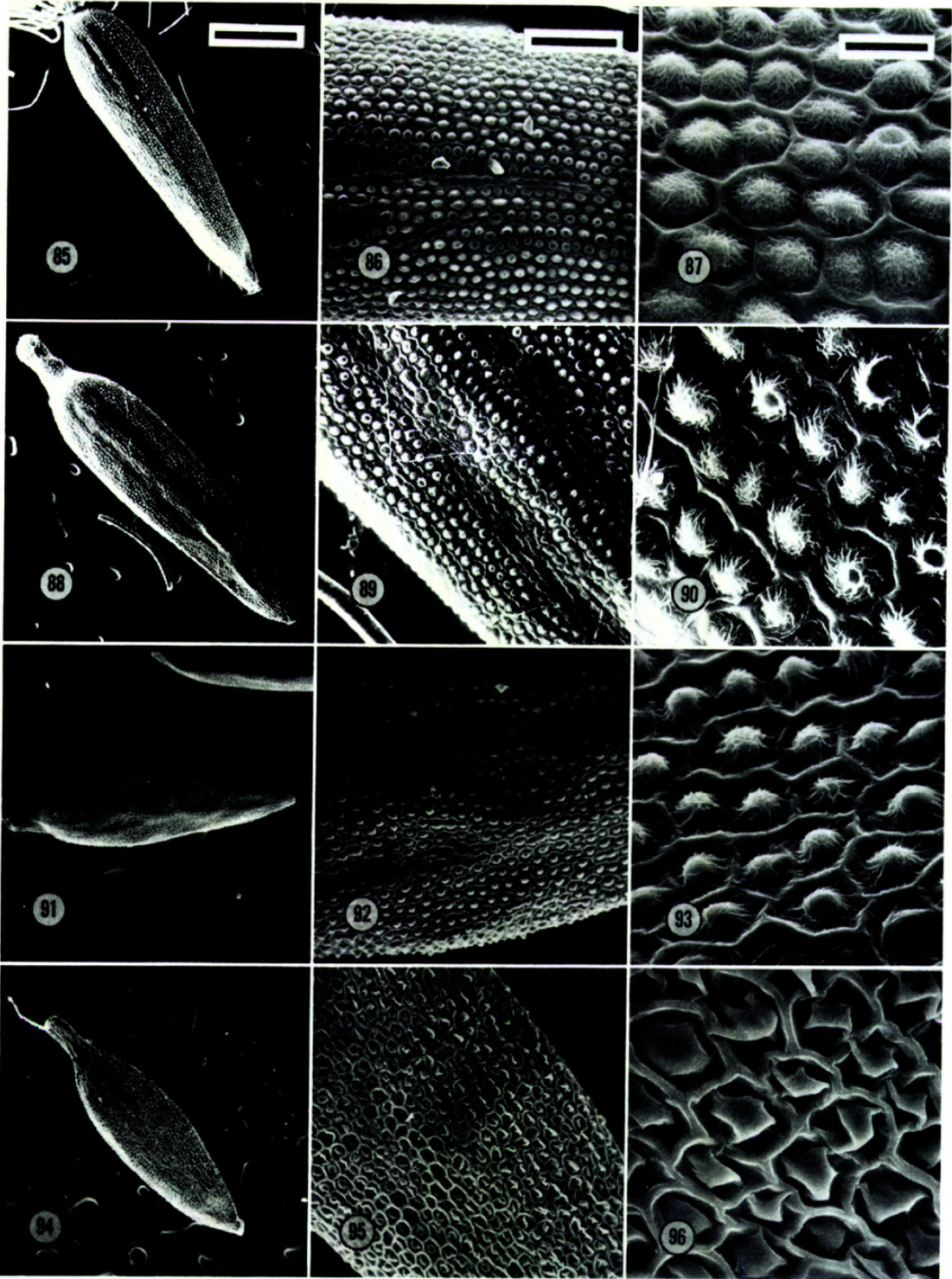
The range in size of this remaining group of species extends from approximately 0.5 mm long for *E. denticulatum* (Figs. 64–66), *E. komarovianum* (Figs. 121–123), and *E. pictum* (Figs. 124–126) to approximately 1.5 mm for *E. cf. pauciflorum* (Figs. 61–63), *E. pylaieanum* (Figs. 88–90), and *E. strictum* (Figs. 85–87). The range in shape of this group of species extends from the obovoid seeds of *E. hirsutum* (Figs. 112–114) and *E. obscurum* (Figs. 109–111) to the narrowly obovoid seeds of *E. strictum* (Figs. 85–87) and *E. shiroumense* (Figs. 49–51). In overall shape, *E. gunnianum* (Figs. 118–120) stands out as having an extended, flat ventral surface which extends beyond the outline of the main body of the seed.

In many species the cells in the region of attachment of the coma proliferate to varying degrees, thus forming a distinct neck. This neck is clearly evident in dorsal view in *E. alsinifolium* (Figs. 145–147), *E. anagallidifolium* (Figs. 148–150), *E. atlanticum* (Figs. 127–129), *E. chilense* (Figs. 172–174), *E. ciliatum* (Figs. 169–171), *E. denticulatum* (Figs. 64–66), *E. hirtum* (Figs. 73–75), *E. hornemannii* (Figs. 136–138), *E. oreganum* (Figs. 160–162), *E. oregonense* (Figs. 76–78), *E. scalare* (Figs. 154–156), and *E. shiroumense* (Figs. 49–51). This neck may exceed 0.2 mm in *E. davuricum* (Figs. 94–96) and *E. pylaieanum* (Figs. 88–90). Although the neck may not be seen as a distinct region in some species when viewed from directly above with the seed lying flat, it can be discerned if the seed is tilted (e.g., *E. watsonii*, Figs. 157, 202).

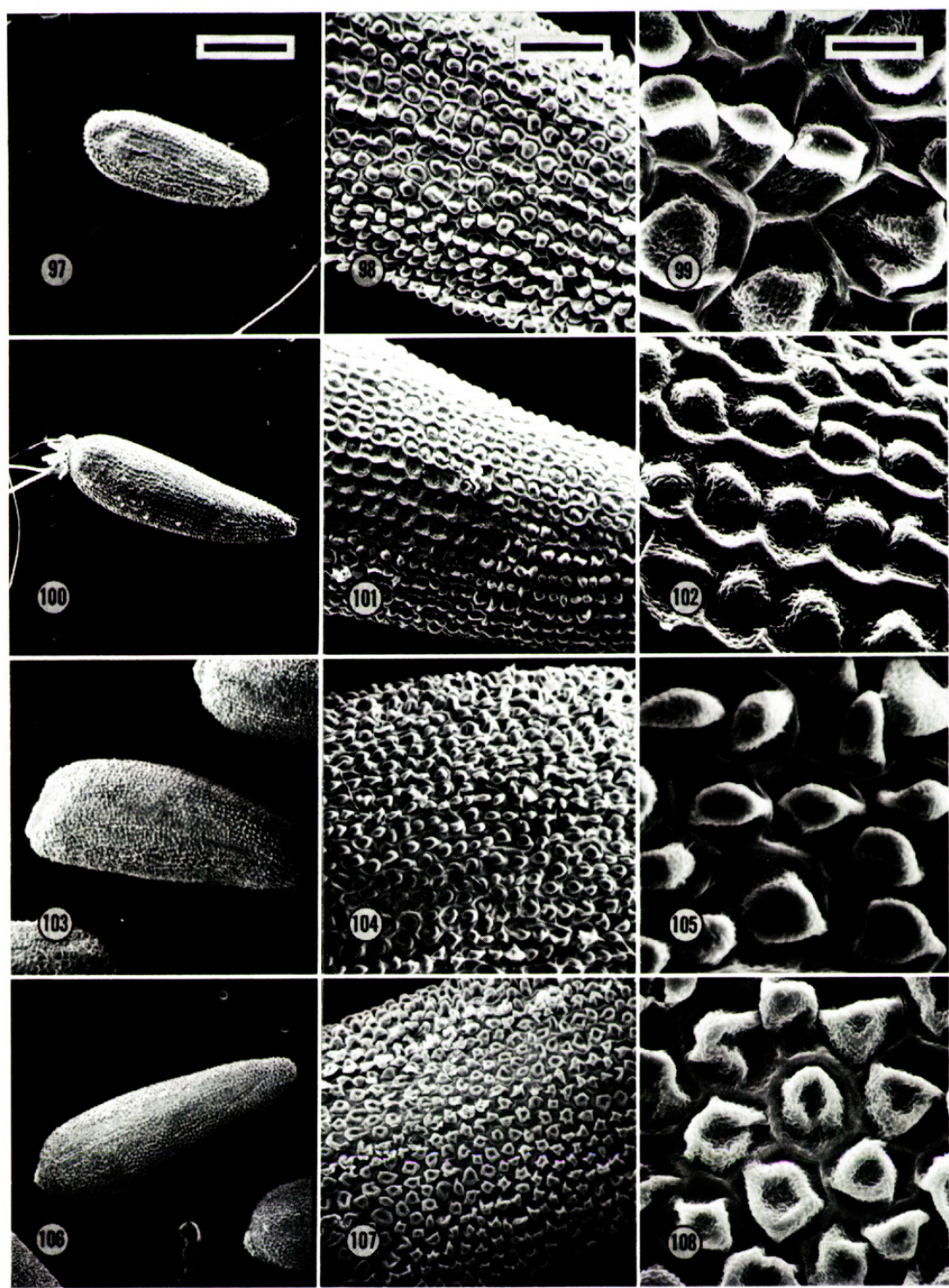
The neck region may be a moderately thick extension of the chalazal end cells (e.g., *E. strictum*, Fig. 203; *E. exaltatum*, Fig. 205) or it may be relatively thin, in which case it is displaced toward the ventral side (e.g., *E. anagallidifolium*, Fig. 204; *E. oregonense*, Fig. 206; *E. scalare*, Fig. 207). In species with the longest necks, the neck cells appear individually elongated (e.g., *E. davuricum*, Fig. 208). The individual trichomes of the coma are usually inserted at the very apex of the neck, although they are occasionally inserted over a broader area (e.g., *E. palustre*, Fig. 210). If the neck is relatively thin, as in *E. exaltatum* (Fig. 205) or *E. watsonii* (Fig. 202), it is sometimes pellucid.

There are three types of surface cells in sect. *Epilobium*: *papillose* (Group I; Berggren, 1974), cells with a convex portion centrally located on the tangential wall, variously shaped and isolated from its neighboring cells by a prominent radial wall reticulum; *foveolate* (Denford & Karas, 1974; Group III; Berggren, 1974), cells lacking any prominent feature other than the raised, regularly polygonal radial walls; and *ridged* (Group II; Berggren, 1974), cells with a centrally located convex portion which is laterally compressed and fused with the raised portions of neighboring cells, forming longitudinal ridges along the length of the seed.

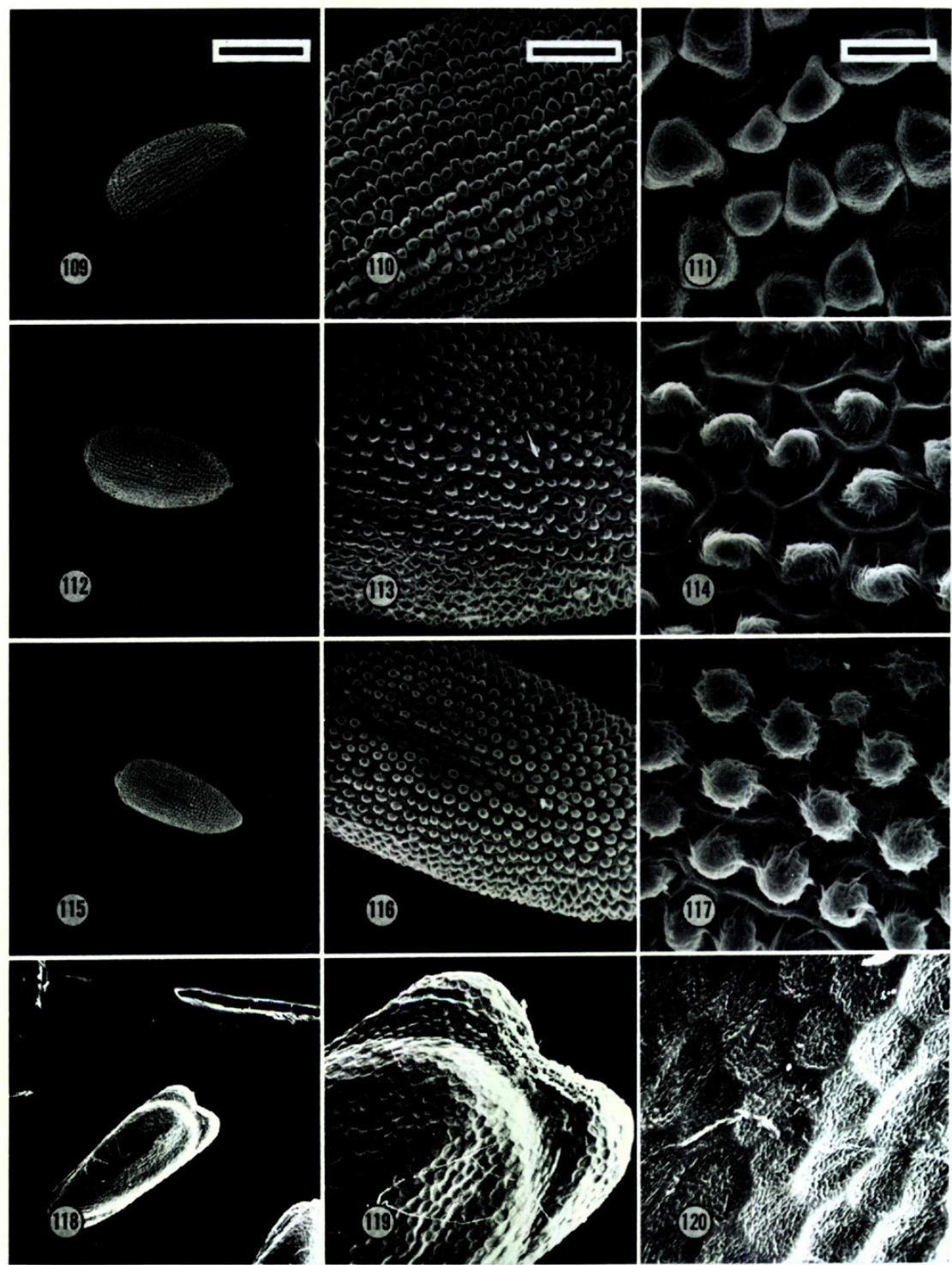
Most species of sect. *Epilobium* have papillose seeds. The central papilla of the surface cells of many species is irregularly compressed into a multisided prominence as in *E. alpestre* (Figs. 103–105), *E. amurense* (Figs. 97–99), *E. obscurum* (Figs. 109–111), *E. shiroumense* (Figs. 49–51), and *E. stereophyllum*



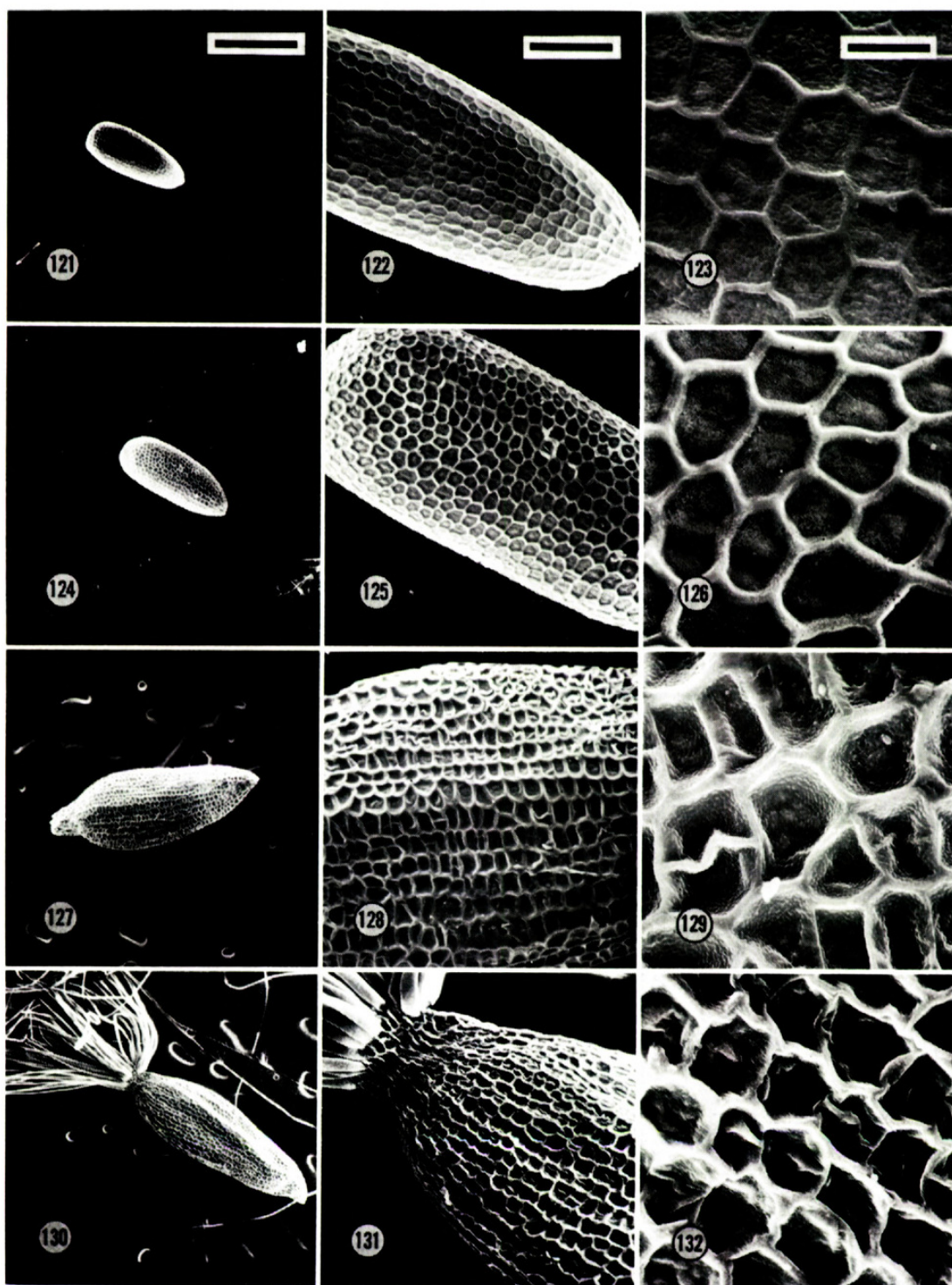
FIGURES 85-96. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—85-87. *E. strictum*.—88-90. *E. pylaeanum*.—91-93. *E. davuricum*, Porsild 306.—94-96. *E. davuricum*, Yurtsev & Raszhivin in 1972.



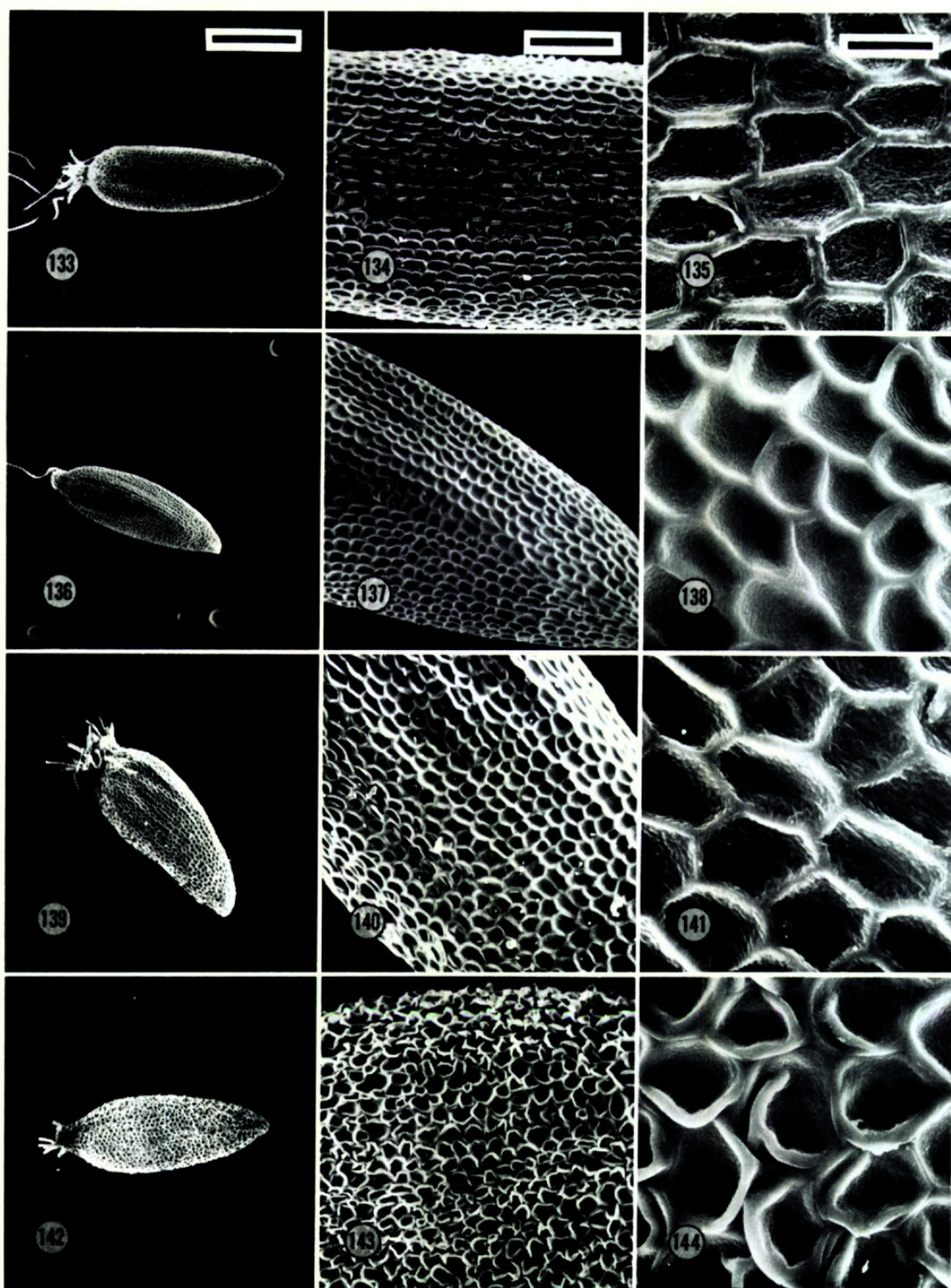
FIGURES 97–108. Scanning electron micrographs of seeds of Eurasian species of *Epilobium* sect. *Epilobium*.—97–99. *E. amurense*.—100–102. *E. pyrricholophum*.—103–105. *E. alpestre*.—106–108. *E. duriaci*.



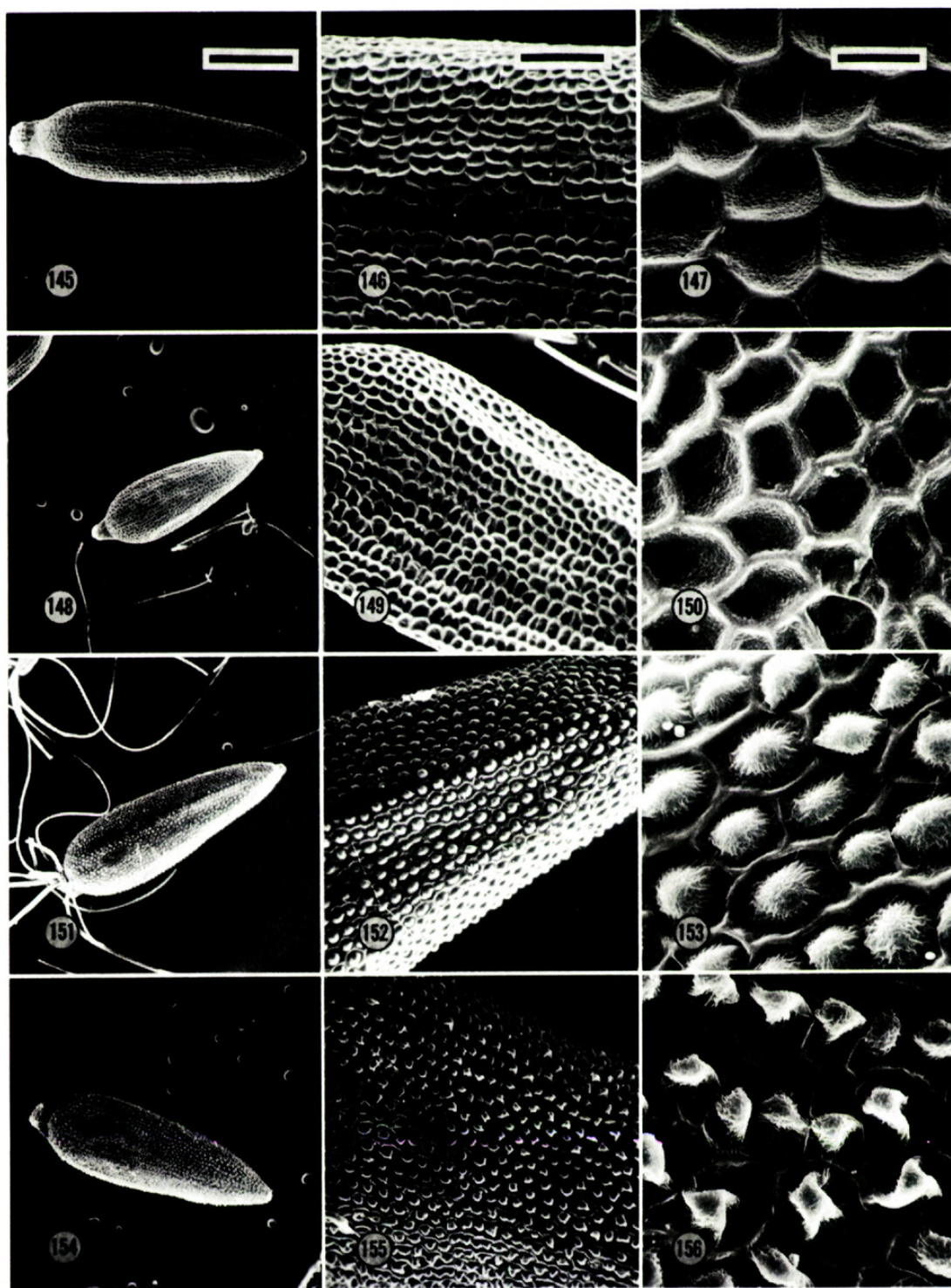
FIGURES 109–120. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—109–111. *E. obscurum*.—112–114. *E. hirsutum*.—115–117. *E. billardierianum* subsp. *billardierianum*.—118–120. *E. gunnianum*.



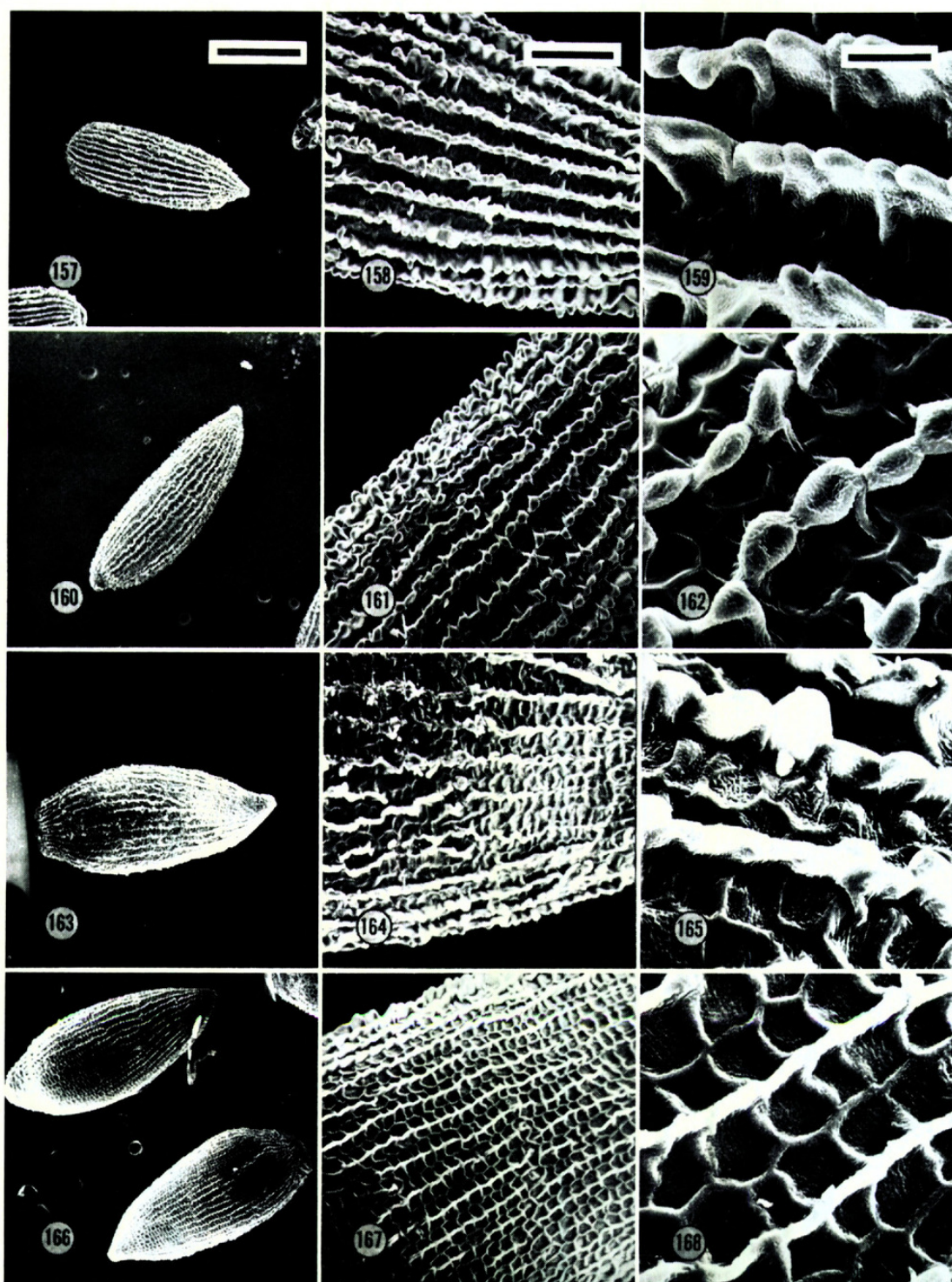
FIGURES 121–132. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—121–123. *E. komarovianum*.—124–126. *E. pictum*.—127–129. *E. atlanticum*.—130–132. *E. nutans*.



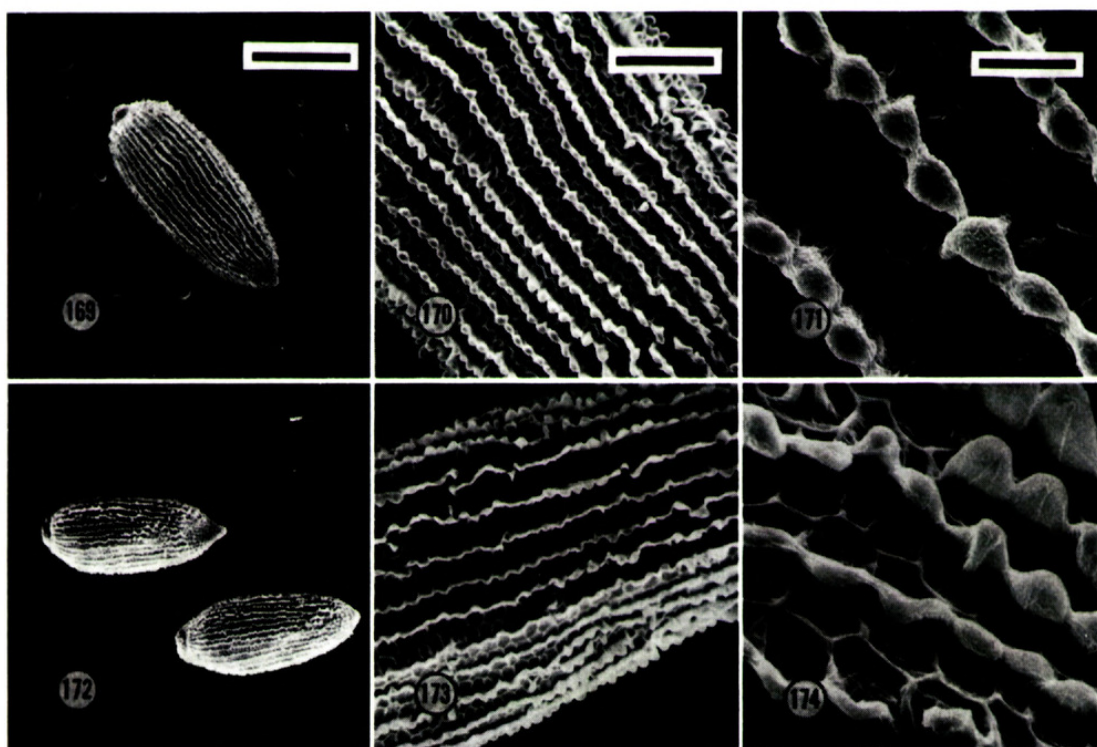
FIGURES 133–144. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—133–135. *E. behringianum*.—136–138. *E. hornemannii* s. lat.—139–141. *E. luteum*.—142–144. *E. treleasianum*.



FIGURES 145–156. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—145–147. *E. alsinifolium*.—148–150. *E. anagallidifolium*.—151–153. *E. nesophilum*.—154–156. *E. scalare*.



FIGURES 157-168. Scanning electron micrographs of seeds of North American species of *Epilobium* sect. *Epilobium*.—157-159. *E. watsonii*.—160-162. *E. oreganum*.—163-165. *E. exaltatum*, M409.—166-168. *E. exaltatum*, M559.

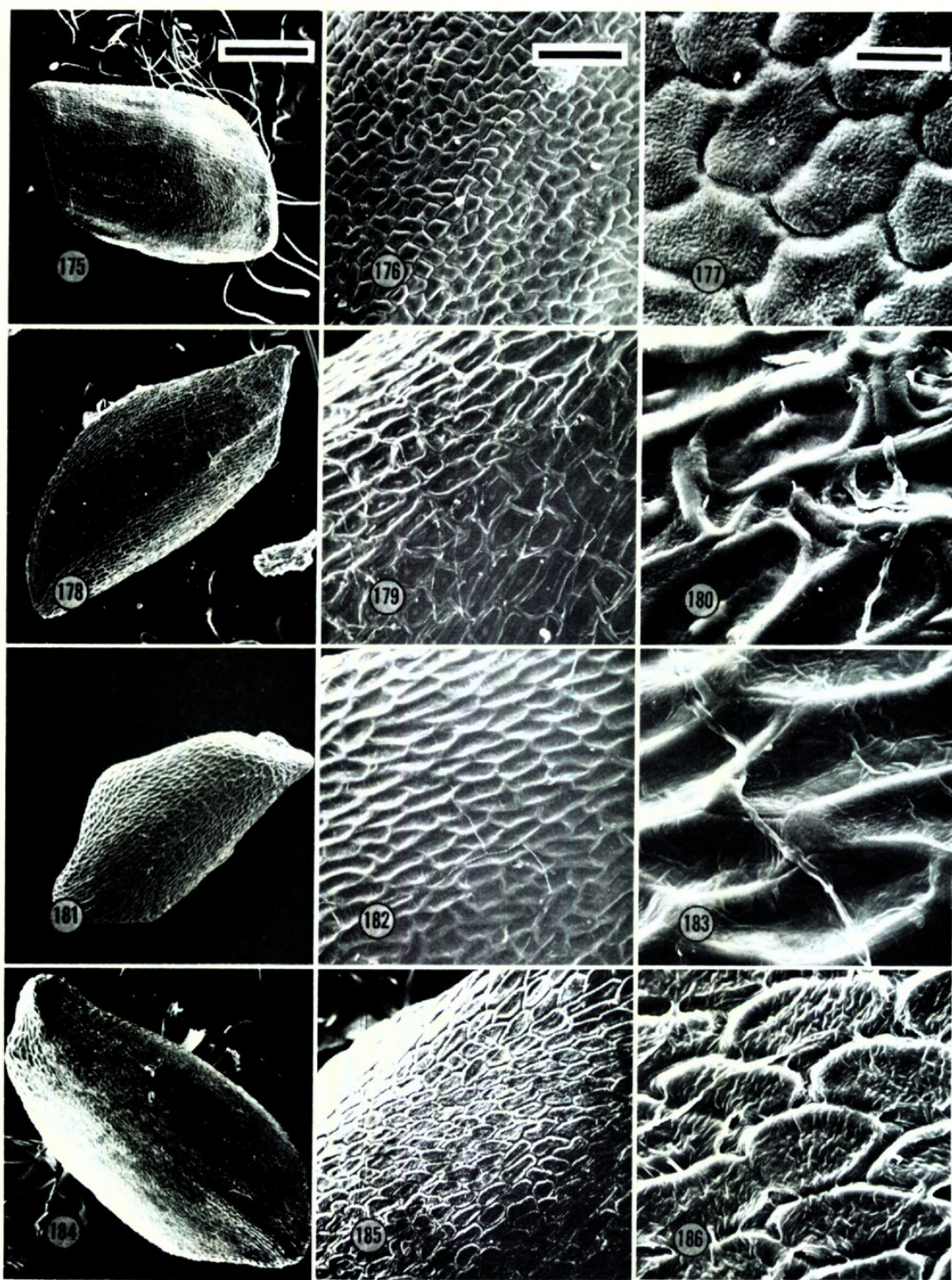


FIGURES 169–174. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—169–171. *E. ciliatum*.—172–174. *E. chilense*.

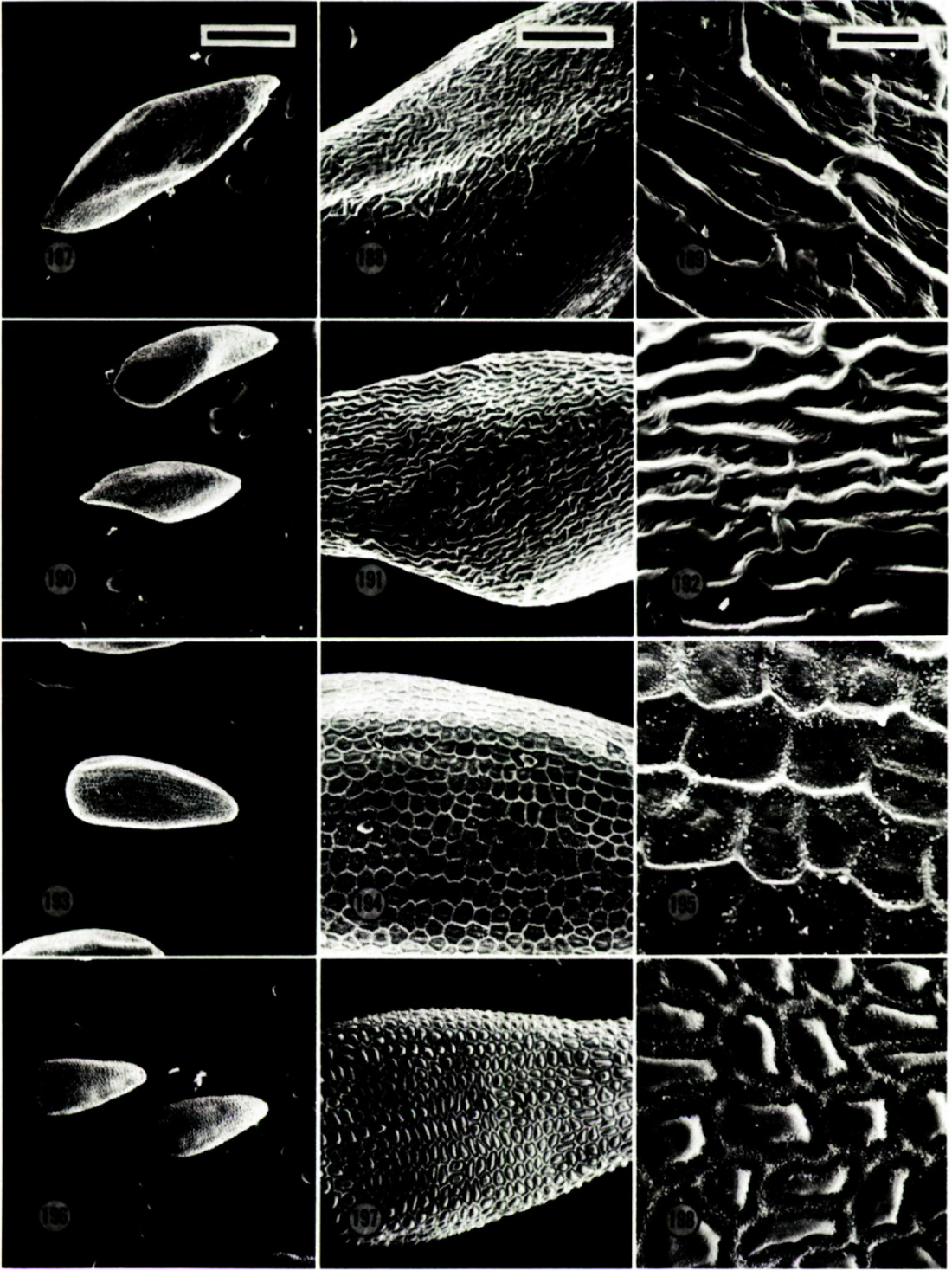
(Figs. 58–60), whereas in others it remains more regularly domeshaped, as in *E. denticulatum* (Figs. 64–66), *E. fauriei* (Figs. 52–54), *E. glaucum* (Figs. 67–69), and *E. pyrricholophum* (Figs. 100–102). In some species, the papilla is marked by radial lines which appear as fine ridges, as in *E. oregonense* (Figs. 76–78), *E. pylaieanum* (Figs. 88–90), some samples of *E. billardierianum* (Figs. 115–117), *E. davuricum* (Figs. 91–93), *E. hirsutum* (Figs. 112–114), and *E. nesophilum* (Figs. 151–153). The papilla of some species, such as *E. leiophyllum* (Figs. 82–84) and *E. duriaei* (Figs. 106–108), is collapsed in the center. The surface cells are usually arranged in irregular rows running longitudinally the length of the seed, but in some species, such as *E. amurense* (Figs. 97–99), *E. fauriei* (Figs. 52–54), and *E. obscurum* (Figs. 109–111), the rows are distinctly regularly arranged.

In foveolate seeds the regularly polygonal reticulum formed by the radial walls is the most prominent feature of the seed surface. This radial wall reticulum is relatively low on the seeds of *E. gunnianum* (Figs. 118–120), and *E. komarovianum* (Figs. 121–123), but more pronounced on the seeds of *E. alsinifolium* (Figs. 146–147), *E. anagallidifolium* (Figs. 148–150), *E. atlanticum* (Figs. 127–129), *E. behringianum* (Figs. 133–135), *E. hornemannii* (Figs. 136–138), *E. luteum* (Figs. 139–141), *E. nutans* (Figs. 130–132), and *E. pictum* (Figs. 124–126).

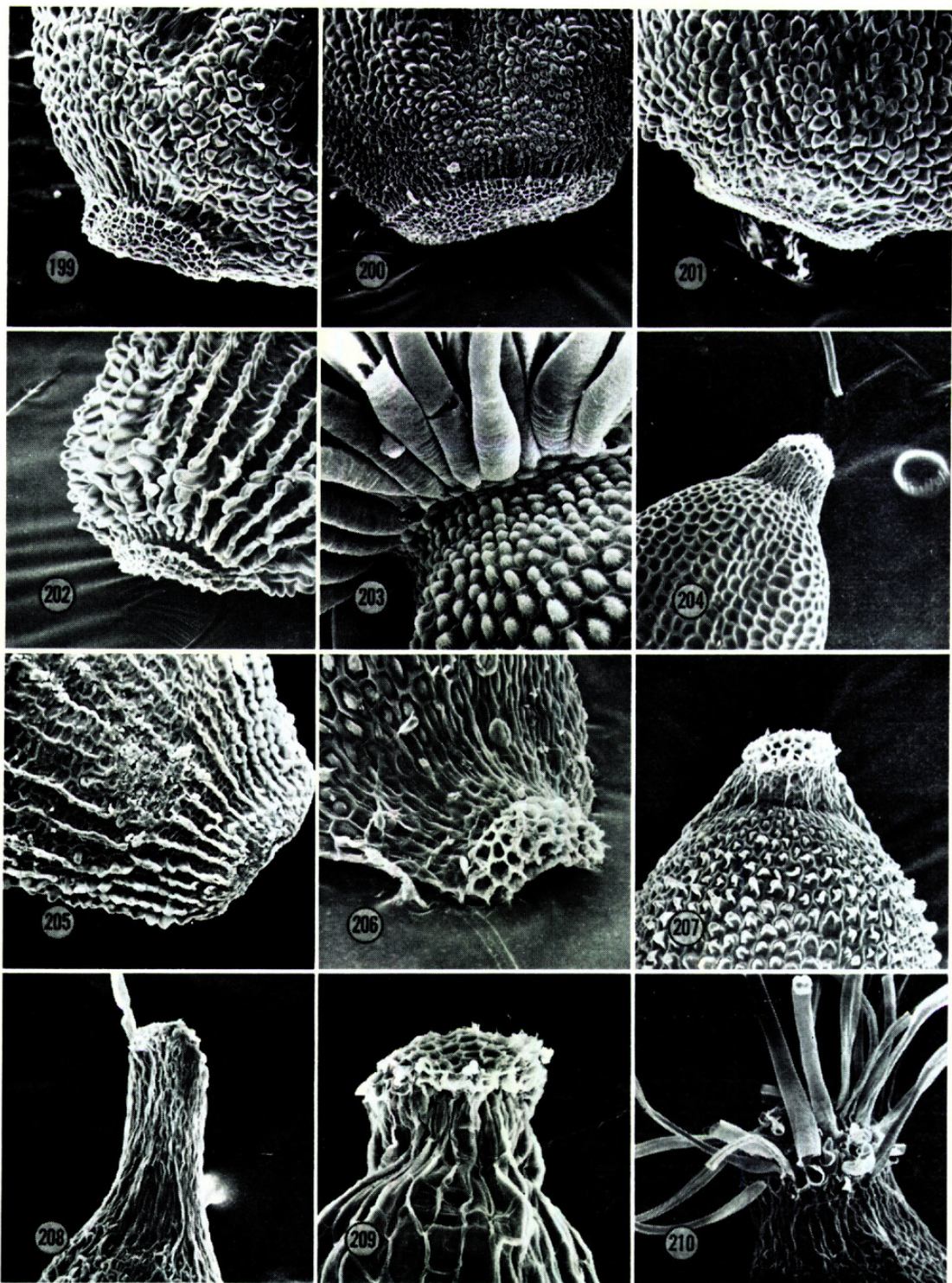
Ridged seeds, marked by longitudinal rows of laterally compressed, fused ridges, are found principally in North American species. Among these are *E. ciliatum* (Figs. 169–171), *E. exaltatum* (Figs. 163–165), *E. oreganum* (Figs. 160–162), and *E. watsonii* (Figs. 157–159). The South American *E. chilense*



FIGURES 175–186. Scanning electron micrographs of seeds of the four species of *Boisduvalia* sect. *Boisduvalia*.—175–177. *B. densiflora*.—178–180. *B. macrantha*.—181–183. *B. stricta*.—184–186. *B. subulata*.



FIGURES 187–198. Scanning electron micrographs of seeds of the species of *Boisduvalia* sect. *Currantia* and *Epilobium* sect. *Crossostigma*.—187–189. *Boisduvalia cleistogama*.—190–192. *B. glabella*.—193–195. *Epilobium minutum*.—196–198. *E. foliosum*.



FIGURES 199–210. Scanning electron micrographs showing variation in chalazal end of seeds of *Epilobium*, including the development of more or less pronounced beaks. All taxa are members of sect. *Epilobium* except as indicated in parentheses following their names.—199. *Epilobium canum* subsp. *canum* (*Zauschneria*).—200. *E. rigidum*, Curtis l.—201. *E. obcordatum* subsp. *obcordatum*.—202. *E. watsonii*.—203. *E. strictum*.—204. *E. anagallidifolium*.—205. *E. exaltatum*.—206. *E. oregonense*.—207. *E. scalare*.—208. *E. davuricum*, Yurtsev & Raszhivin in 1972.—209. *E. angustifolium*.—210. *E. palustre*.

(Figs. 172–174) likewise has ridged seeds. The seeds of hybrids between species with ridged and papillose seeds are intermediate in various ways and have been illustrated by Skvortsov & Rusanovich (1973).

II. *Boisduvalia*

The seeds of *Boisduvalia* are distinct from those of *Epilobium*. Their shape, which is irregularly angular-fusiform, is unique, as is the structure of their surface cells. The relatively broad seeds of *B. densiflora* (Figs. 175–177) and *B. subulata* (Figs. 184–196) have surface cells which are slightly raised, flat, and irregularly polygonal. The seeds of *B. macrantha* (Figs. 178–180), *B. stricta* (Figs. 181–183), and the narrower seeds of *B. cleistogama* (Figs. 187–189) and *B. glabella* (Figs. 190–192), have surfaces that are covered by an irregularly striated reticulum composed of the unevenly joining radial walls of the surface cells.

DISCUSSION

A number of distinct seed types occur in the genera *Boisduvalia* and *Epilobium*, as will be discussed below. In both genera, as in other Onagraceae, the surface architecture is made up of the regularly repeated structures of individual surface cells. The characteristic forms of these surface cells are the result of differential thickening in their walls, as thin sections of the seeds of *Epilobium* (Ky-tövuori, 1972; Denford & Karas, 1974) demonstrate; seed coat patterns in many other genera are comparable, for example in *Cordylanthus* (Chuang & Heckard, 1972), Melastomataceae (Whiffin & Tomb, 1972), and *Mentzelia* (Hill, 1976), as well as other investigations reviewed by Brisson & Peterson (1976).

There is a major contrast in Epilobieae between the angular-prismatic seeds of *Boisduvalia*, which lack a coma, and the regularly obovoid, flattened ones of *Epilobium*, which have a coma in all taxa except in a few in which it has been lost. In addition, the surface cells in *Boisduvalia* are irregular and thus unlike any found in *Epilobium*. Those of *B. densiflora* ($n = 10$) and *B. subulata* ($n = 19$) are low, flat, and irregularly polygonal, whereas those of *B. macrantha* ($n = 10$) and its probable aneuploid derivative *B. stricta* ($n = 9$; Raven & Moore, 1965) are concave and have radial walls that are longitudinally striate and irregularly thickened. These four species comprise sect. *Boisduvalia* (Raven, 1976); the remaining two species, which comprise sect. *Currania* ($n = 15$), have seeds that resemble those of *B. macrantha* and *B. stricta*, although they are smaller.

In *Epilobium*, it is convenient to recognize seven distinct types of seeds, and these will be discussed in turn.

1. Large, obovoid, constricted. In sects. *Cordylophorum*, *Xerolobium*, and *Zauschneria*, the seeds are obovoid, large, and more or less prominently constricted toward the micropylar end. Their surface is made up of cells which are smooth and convex, with obscure lateral walls (Figs. 1–24). The relatively prominent side walls in our preparation of *E. canum* subsp. *canum* probably are associated with shrivelling. The five species that comprise these three sections are

relictual (Raven, 1976), and this seed type is almost certainly primitive for *Epilobium*. In sect. *Epilobium*, with some 185 species and a worldwide distribution, it occurs only in *E. rigidum* (Figs. 37–39, 40–42), a large-flowered, xerophytic species of the Siskiyou Mountains of northwestern California and adjacent Oregon. The Siskiyou Mountains are a well known relict area (Whittaker, 1960), and *E. rigidum* very likely resembles the basic stock from which the remaining species of sect. *Epilobium* have diverged. As in *E. nevadense*, *E. nivium*, and *E. paniculatum*, the subtending bracts in *E. rigidum* are fused to their pedicel in all but the lowermost flowers. The phylogenetic significance of this observation remains to be determined.

2. Papillose. Most species of sect. *Epilobium* have seeds that are smaller, papillose, obovoid to narrowly obovoid, and lack a micropylar constriction. The lateral walls of their surface cells are prominent. These include *E. obcordatum* (Figs. 43–45, 46–48), the species most closely related to *E. rigidum* and, like it, a large-flowered xerophyte of the western United States. In addition, the four species of sect. *Chamaenerion* subsect. *Rosmarinifolium*, exemplified by *E. dodonaei* (Figs. 34–36) and *E. stevenii* (Figs. 31–33), have this seed type. It seems clearly to have evolved from the first type and to have given rise in turn to all of the other more specialized seed types within the genus, with the probable exception of that found in sect. *Crossostigma*. The tribe Epilobieae seems to have consisted initially of xerophytes, from which the more widespread and numerous mesophytic and hydrophytic species were derived. Perhaps an evolutionary trend toward more numerous, smaller seeds accompanied the exploitation of such habitats.

Seeds of this type characterize more than a hundred species, including the European *E. alpestre*, *E. collinum*, *E. duriaei*, *E. hirsutum*, *E. lanceolatum*, *E. montanum*, *E. nervosum*, *E. obscurum*, *E. parviflorum*, *E. roseum*, and *E. tetragonum*, as well as the circumboreal *E. davuricum* and *E. palustre* (Skvortsov & Rusanovitch, 1974; Berggren, 1974; this paper). Papillose seeds also occur in the Asian *E. amurense*, (Figs. 97–99), *E. fauriei* (Figs. 52–54), *E. platystigmatosum* (Figs. 55–57) and *E. pyrricholophum* (Figs. 100–102); the South American *E. denticulatum* (Figs. 64–66), *E. glaucum* (Figs. 67–69), *E. hirtum* (Figs. 73–75), *E. cf. pauciflorum* (Figs. 61–63), and one unidentified species (South American species # 1, Figs. 70–72); the African *E. stereophyllum* (Figs. 58–60); the Australasian *E. billardierianum* (Figs. 115–117); and the North American *E. coloratum* (Figs. 79–81), *E. oregonense* (Figs. 76–78), *E. pylaeanum* (Figs. 88–90), and *E. strictum* (Figs. 85–87), as well as most populations of *E. saximontanum* Hausskn. Although only one Australasian species of this first type of surface structure is illustrated in this paper, most species of this region have seeds of this type (Raven & Raven, 1976).

Many of the microstructural details of papillose seeds are strikingly constant from one sample to another. The convex portion of the surface cells of *E. hirsutum* (Figs. 112–114), for example, are characterized by spirally arranged radial lines, as illustrated by Skvortsov & Rusanovitch (1974; fig. 1C). Similarly, the surface cells of *E. nesophilum* (Figs. 151–153), and the closely related *E. pylaeanum* (Figs. 88–90) and *E. davuricum* (Figs. 91–93) have characteristically

low convex tangential walls with radial lines as illustrated in Skvortsov & Rusanovitch (1974: figs. 2E, F, and fig. 2G, respectively), although considerable variability in surface structure within these two species is also evident in both studies (e.g., *E. davuricum*, Figs. 91–93, 94–96).

Nearly all of the species with papillose seeds in sect. *Epilobium*, well over a hundred, have the BB chromosome arrangement (Seavey & Raven, 1976; unpublished). Among the exceptions are the Asian *E. fauriei*, *E. platystigmatosum*, and *E. shiroumense*, as well as most populations of the circumboreal *E. hornemannii* s. lat. and the North American *E. clavatum* Trel., all of which have the CC arrangement. In addition, some of the species with the AA chromosome arrangement, including the South American species of the group *Denticulata* (Samuelsson, 1923, 1930) and the North American *E. glaberrimum* Barbey and *E. brevistylum* Barbey, as well as *E. saximontanum*, also have papillose seeds. Both the AA and CC chromosome arrangements differ from BB by one reciprocal translocation, and we believe that each may be independently derived from BB. On the basis of the evidence presented here, it appears that the common ancestor of each of these groups had papillose seeds.

Most species of Haussknecht's (1884) group *Palustriformes*, including *E. davuricum* (Figs. 91–93, 94–96, 208), *E. palustre* (Fig. 210), and *E. pylaieanum* (Figs. 88–90) among those illustrated in the present study, have an exaggerated beak at the chalazal end of the seed; although others, such as *E. strictum*, which undoubtedly belongs to this group, do not (Figs. 85–87, 203). The *Palustriformes* have the BB chromosome arrangement and papillose seeds in all taxa; similar in these respects is *E. oregonense* (Figs. 76–78). *Epilobium scalare*, a Newfoundland endemic that has been collected only once, has papillose seeds and a prominent beak also but does not resemble *Palustriformes* in most respects. Chalazal beaks are discussed in general on p. 30 and illustrated in Figs. 199–210.

3. Foveolate. By flattening of the central papilla found in the surface cells of the seeds of the preceding group, foveolate seeds (Danford & Karas, 1974) have evolved. Such seeds, as viewed with a 20× lens, have usually been described as "smooth" in taxonomic papers on *Epilobium*. Some species, including the New Zealand *E. alsinoides* (different subspecies), have some populations with papillose seeds and others with foveolate seeds. The same occurs in the circumboreal *E. hornemannii* s. lat. and in the North American *E. clavatum*. It appears, therefore, that the evolution of foveolate seeds has taken place repeatedly within the genus.

In Australasia, where all species have the BB chromosome arrangement and presumably evolved from a common ancestor (Raven & Raven, 1976), 31 species have papillose seeds; 10, including *E. komarovianum* (Figs. 121–123) and *E. pictum* (Figs. 124–126) have foveolate seeds; *E. alsinoides*, already mentioned, has both papillose and foveolate seeds in different subspecies; and 4 species, including *E. gunnianum* (Figs. 118–120) have a distinctive seed type that will be discussed below. In almost every one of the 11 species in which foveolate seeds occur, these appear to have evolved separately from papillose seeds (Raven & Raven, 1976).

In North America, foveolate seeds occur in *Epilobium luteum*, a rather iso-

lated species, and in some populations of the *E. glandulosum* complex (AA). In addition, they are characteristic of some or all populations of several entities in the CC group: *E. anagallidifolium* (Figs. 148–150), *E. behringianum* (Figs. 133–135), *E. clavatum*, and *E. hornemannii* s. lat. (Figs. 136–138). The seeds of *E. treleasianum* may be papillose (Figs. 142–144) or foveolate, owing to the hybrid nature of *E. treleasianum*, a series of populations of hybrid origin between *E. luteum* (seeds foveolate) and other species (Seavey, in preparation). Papillose seeds appear to be dominant in a genetic sense over foveolate ones.

Among the species that occur in Europe, only species of the CC (*Alpinae*) group and three other species—*E. nutans* (BB in part; Figs. 130–132), *E. atlanticum* (AA; Figs. 127–129), and *E. alsinifolium* (AA; Figs. 145–147)—have foveolate seeds. Judged from the wide morphological gap between the latter two species and the different chromosome arrangement in the first, it is likely that all evolved foveolate seeds independently. The fact that all three are species of low stature that occur in alpine habitats, like the species of group *Alpinae* (here defined to comprise only CC species and therefore to exclude *E. alsinifolium*), suggests that some common selective force may favor foveolate seeds under such conditions. The third European species with the AA chromosome arrangement, *E. alpestre* (Figs. 103–105), has papillose seeds.

4. Obovoid-patelliform. Four Australasian species—*E. gunnianum* (Figs. 118–120), *E. curtisiae* Raven, *E. willisii* Raven & Engelhorn, and *E. angustum* (Cheesem.) Raven & Engelhorn—have distinctive seeds with a hollow ring around their adaxial side, which are thus patelliform. The first three are probably closely related, but the occurrence of similar seeds in *E. angustum*, apparently closely related to *E. komarovianum*, has not been explained satisfactorily (Raven & Raven, 1976). The seeds of *E. willisii* and of many populations of *E. gunnianum* are finely papillose, those of the other taxa foveolate. The obovoid-patelliform seed type undoubtedly evolved from the more frequent papillose type within Australasia.

5. Irregularly reticulate. The three species of sect. *Chamaenerion* subsect. *Leiostylae* have seeds in which the very thin radial walls of the epidermal cells of the seed coat form an irregularly polygonal reticulum (Figs. 25–30). The four other species of sect. *Chamaenerion*, comprising subsect. *Rosmarinifolium*, have papillose seeds that resemble those of most species of sect. *Epilobium* in size and shape. The close relationship of the two subsections of sect. *Chamaenerion* is beyond question in that they share the following unique or highly unusual characteristics for the genus: all leaves spirally arranged, flowers zygomorphic, floral tube obsolete, pollen shed singly. This indicates unequivocally that the unusual seeds of subsect. *Leiostylae*, stressed by Skvortsov & Rusanovitch (1974) and by Brisson & Peterson (1976) as an argument for the generic distinctness of sect. *Chamaenerion*, represent instead an evolutionary specialization within this group, otherwise characterized by seeds similar to those of many species of sect. *Epilobium*. Also implied by the seed morphology of subsect. *Rosmarinifolium* is the divergence of sect. *Chamaenerion* from an ancestor that would be placed within sect. *Epilobium* long after the divergence of sects. *Cordylophorum*, *Xerolobium*, and *Zauschneria* from species such as *E. rigidum*. Additional evidence for

the close relationship of sect. *Chamaenerion* with sect. *Epilobium* is summarized by Raven (1976).

6. Ridged. Within the North American group of species with the AA chromosome arrangement (Seavey & Raven, 1976), there has originated a distinctive seed type, described above, that doubtless delimits a phylogenetically coherent group of taxa. Illustrated here are *E. ciliatum* (Figs. 169–171; extends to Japan), *E. exaltatum* (Figs. 163–165), *E. oreganum* (Figs. 160–162), and *E. watsonii* (Figs. 157–159). *Epilobium ciliatum* occurs as an adventive in Europe and in Australasia (Raven & Raven, 1976), and its seeds have been illustrated several times (as *E. adenocaulon* Hausskn., Troughton & Donaldson, 1972: pls. 103–104; Skvortsov & Rusanovitch, 1973, 1974; Berggren, 1974; Raven & Raven, 1976). Virtually identical seeds occur in the South American *E. chilense* (Figs. 172–174), this suggesting recent immigration to South America following the origin of the group in North America. Within the *Epilobium glandulosum* complex foveolate seeds also occur, but these have probably been derived from ridged ones. The most primitive species of this group is apparently a local endemic of bogs in the Siskiyou Mountains, *E. oreganum*, which has exerted, deeply 4-lobed stigmas.

Denford & Karas (1974) have interpreted the ridges in seeds of this type as being formed of rows of flattened papillose cells flanked on both sides by foveolate cells. Our SEM observations, however, show clearly that the ridges are instead formed of the finlike central portions of individual surface cells, all such cells on the abaxial side of the seed being similar. No foveolate cells were observed on the abaxial surface of these seeds.

7. Finely papillose. The distinctive seeds of sect. *Crossostigma*, described on p. 23 and by Seavey et al. (1977), cannot easily be related to any other seed type in the genus, and the relationships of the two annual species included in this section are obscure.

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