

The Northwest European Pollen Flora, 43

POLYGONACEAE

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Literature

Ananova (1958), Crompton and Parmelee (1978), Borodina (1979), Borzova and Sladkov (1969), Erdtman (1943, 1952, 1969), Berglund and Praglowski (1961), Florin (1969), Hedberg (1946), Huang (1972), Hyde and Adams (1958), Kuprianova and Alyoshina (1978), Loeve (1940) Markgraf and D'Antoni (1978), Miyoshi and Morita (1986), Moore and Webb (1978), Nair (1965), Nair et al. (1977), Nowicke and Skvarla (1977), Surova (1975), Ting-Su (1949), Visset (1977), Wodehouse (1935), Van Zinderen Bakker (1956).

Introduction

The family Polygonaceae consists of some 40 genera with ca. 800 species. Its distribution is cosmopolitan, but chiefly in the northern temperate regions (Engler, 1964). The Polygonaceae are of special interest as some of its members are grown as crops (e.g. *Fagopyrum esculentum*, *Rheum officinale*), while others are well-known weeds (e.g. *Polygonum aviculare*, *Rumex acetosella*). According to Nowicke and Skvarla (1977) the Polygonaceae is one of the most eurypalynous families among the dicotyledons (see also Wodehouse, 1930; Hedberg, 1946; Erdtman, 1961).

In the Flora Europaea (Tutin, 1964) the genus *Polygonum* is split up into smaller units; the genera *Bilderdykia* Dumortier (syn. *Fallopia* Adanson) and *Reynoutria* Houttuyn are all accepted. Van der Meijden (in Heukels and Van der Meijden, 1983) combines these genera with the genus *Polygonum* as he considered the differences too small to justify splitting up the genus. In the present paper Van der Meijden's view is followed.

An extensive study of the pollen morphology in the Polygonaceae was published by Wodehouse (1931). He described several species from a range of North American genera with an explanation of "developmental tendencies" and also a key to the species. However, most of

the species described, do not occur in North-west Europe. Hedberg (1946), in his classic paper on pollen morphology in the genus *Polygonum*, described ten main pollen types and a number of aberrant types. He proposed a new taxonomic classification based on pollen morphology and gave a key to the pollen types.

According to Godwin (1975), pollen grains of *Polygonum* and *Rumex* appear for the first time in the Hoxnian (= Holsteinian) and Pastonian (= early Cromerian) interglacials respectively. They are two of the familiar indicators of the Devensian (= Weichselian) periglacial vegetation. Pollen grains of *Rumex* are moreover indicative of woodland clearance and the spread of agriculture in the sub-boreal period (Holocene). *Koenigia islandica* and *Oxyria digyna*, two taxa rather common in arctic areas, were also found in England during the Devensian glacial. Andersen (1961) also recognized several different pollen types in his material from the Weichselian glacial in Denmark. He based his identifications of polygonaceous pollen types on Hedberg's (1946) data and consequently recognized a restricted number (e.g. *Bistorta* type, *Persicaria* type). In the genus *Rumex* Andersen examined 18 European species which he could divide into four pollen groups. Further observations on his study are found under the comments on the *Rumex acetosa* type (p.14).

Terminology

Terminology here is based on Reitsma's definitions (1970). Some morphological features, however, encountered in this paper are not mentioned by him and need further explanation. Others are peculiar to the Polygonaceae and also need comment.

(1) Some pollen types show ring-shaped endoapertures in the equatorial plane which were called "ringfurchen" by Wagenitz (1955) and "colpi aequatoriales" by Faegri and Iversen (1964, 1975). Reitsma suggested the latinized word "**endocingulus**" (1966). In the present paper Reitsma's term is used.

(2) Some pollen types have costae endocolpi which are complex, especially in the colpus area. There is a thinned area in the middle of these costae where ectocolpus and endocolpus cross. Its outline is either circular or elliptic. Punt and Rentrop (1974) suggested the term "middle part" for this phenomenon. Dimon (1971) called this feature "aperture moyenne" in her thesis on the Compositae of the Mediterranean. Thanikaimoni (1980) and Vasanthy (1980) introduced the term mesoaperture. This term replaced Dimon's "aperture moyenne" which was a mixture of French and Latin. Thanikaimoni merely mentioned mesoaperture as a replacement of "aperture moyenne", whereas Vasanthy discussed the place of this aperture in the apertural system. As Vasanthy indicated, it is preferable to use the term mesoaperture to indicate the relative position (topography) of the apertural unit. We have chosen the term **mesoaperture** in the present paper.

(3) The terms reticulate, microreticulate and tectum perforate are used according to the definitions of Praglowski and Punt (1973).

(4) Granules are interpreted in this paper as sexine elements of undefined shape and outline, but less than 1 μm in diameter.

(5) Exine and aperture measurements follow the definitions given by Punt (1971). These measurements are:

colpus: **slit-like**, ca. 1 μm wide or less, margins parallel; **narrow**, at least 1–2 μm wide; **broad**,

> 2 μm wide; **short**, in equatorial view colpus ends visible; **long**, in equatorial view colpus ends not visible.

exine: **thin**; < 1.5 μm , **rather thin**, 1.5–2 μm ; **thick**, 2–3 μm ; **very thick**, > 3 μm .

Specimens examined

Bilderdykia convolvulus (L.) Dumortier — syn. *Polygonum convolvulus*.

Bilderdykia dumetorum (L.) Dumortier — syn. *Polygonum dumetorum*.

Fagopyrum esculentum Moench — Belgium: Lejeune et Courtois 556 (U); The Netherlands: Arnolds 1681 (U), Fresh Material Punt Anno 1964, Swart 1831 (U).

Fagopyrum tataricum (L.) Gaertner — The Netherlands: Dornduif s.n. (U), Van Steenis s.n. (U); Sweden: Lundberg s.n. (U).

Koenigia islandica L. — Iceland: Ferman and v.Hille 74 (U), Oosterveld O.1108 (U); Spitsbergen: Van der Knaap, Van Leeuwen, Bogaers and Farjon 27a (U).

Oxyria digyna (L.) Hill — England: Hayes 186 (BM); Greenland: Daniëls, Hooft and De Molenaar D187 (U); Norway: Exc. Biol. Stud. Utrecht 1970–1926 (U).

Polygonum amphibium L. — England: Gerrans 895 (BM); Ireland: Kertland s.n. (U); The Netherlands: Hekking s.n. (U), Fresh Material Punt Anno 1958; Sweden: Holmgren s.n. (S).

Polygonum amplexicaule Don — India: Renu Anand s.n., (U).

Polygonum arenastrum Boreau — Czechoslovakia: Unar 1525 (U); Italy: Exc. Biol. Stud. Utrecht 1966–2623 (U); Norway: Hessel 1242 (U); Spain: Exc. Biol. Stud. Utrecht 1964–635 (U).

Polygonum aviculare L. — England: Wilson 36 (U), Wilmott 534B (BM); Germany: Fresh Material Küster Anno 1982; The Netherlands: Hekking s.n. (U), Swart 259 (U), Fresh Material Punt Anno 1957; Russia: Samoilovitch s.n.

Polygonum bistorta L. — England: Hayes 81 (BM); France: Exc. Biol. Stud. Utrecht 1960–6 (U); Germany: Fresh Material Küster Anno 1982, idem Voorrips Anno 1964; The Netherlands: Dijkstra 640 (U), Ensink s.n. (L), Fresh Material Punt Anno 1957.

Polygonum boreale (Lange) Small — Iceland: Exc. Allerton Gray School 1961–54 (BM); Norway: Williams s.n. (BM).

Polygonum convolvulus L. — England: Gerrans 1294 (BM); Germany: Behrendsen s.n. (U), Fresh Material Küster Anno 1982; Ireland: Hessel, Klein and Rubers 1185 (U); The Netherlands: Van Royen 360 (U), Fresh Material Punt Anno 1957, idem Anno 1962.

Polygonum dumetorum L. — England: Hume 1322 (BM); Italy: Todaro 670 (U); The Netherlands: Fresh Material Punt Anno 1963; Switzerland: Kramer 157 (U).

Polygonum foliosum Lindberg — Finland: Lindberg s.n. (L); Sweden: Svenonius 573 (L).

Polygonum hydropiper L. — England: Bangerter and Hall

- 415 (BM); Ireland: Hessel, Klein and Rubers 1655 (U); The Netherlands: Dijkstra 140 (U), Hekking s.n. (U), Fresh Material Punt Anno 1961.
- Polygonum lapathifolium* L. — England: Mathews s.n. (BM); Ireland: Hessel, Klein and Rubers 1773 (U); The Netherlands: Hekking s.n. (ssp. *brittingeri*) (U), Rubers 1582 (ssp. *lapathifolium*) (U), Fresh Material Punt Anno 1960; Sweden: Blom s.n. (ssp. *lapathifolium*) (U).
- Polygonum maritimum* L. — England: Hunnybun 1427 (BM); France: Sloet and De Fouw 74 (U); Portugal: Bento Rainha 3723 (U).
- Polygonum minus* Hudson — Belgium: Lejeune et Courtois 267 (U); England: Marshall s.n. (BM); Ireland: Hessel, Klein and Rubers I-32 (U); The Netherlands: Koopmans 542 (L), De Visser s.n. (L).
- Polygonum mite* Schrank — England: Gibbons s.n. (BM); The Netherlands: Mennega s.n. (U), Wasscher s.n. (U), Fresh Material Punt Anno 1958, idem Smit Anno 1963.
- Polygonum oxyspermum* Meyer et Bunge ex Ledebour ssp. *oxyspermum* — Sweden: Fries 668 (L).
- Polygonum oxyspermum* Meyer et Bunge ex Ledebour ssp. *raii* (Babington) Webb et Chater — Norway: Alm 54 (BM), Nannfeldt s.n. (L), Samuelson et Zande s.n. (BM).
- Polygonum patulum* Bieberstein — France: Sutter vL 425 (U); The Netherlands: Bakhuizen v.d. Brink 5390 (U).
- Polygonum persicaria* L. — Germany: Miquel s.n. (U); Ireland: Ferguson 2246 (BM); The Netherlands: Dijkstra 457 (U), De Rooy 226 (U), Swart 1846 (U), Fresh Material Rem Anno 1952, idem Punt Anno 1963.
- Polygonum polystachyum* Wallich ex Meissner — The Netherlands: De Jongh Jr. s.n. (L), De Wever s.n. (L).
- Polygonum rurivagum* Jordan ex Boreau — France: Héribaude-Joseph s.n. (BM), Clermont et Rione s.n. (BM); Ireland: Hessel, Klein and Rubers 2206 (U).
- Polygonum viviparum* L. — Austria: Küster Fresh Material Anno 1982; England: Cannon and Herbert 2148 (BM); France: Exc. Biol. Stud. Utrecht 1967-2377 (U); Iceland: Oosterveld 0.916 (U); Norway: Mennega s.n. (U); Sweden: Exc. Biol. Stud. Utrecht 1965-1621 (U).
- Rheum officinale* L. — The Netherlands: Kok-Ankersmit 10 (U).
- Rumex acetosa* L. — Denmark: Exc. Stud. Biol. Utrecht 1956-3; France: Krüger and Bick H.J. 114 (U); Ireland: Hessel, Klein and Rubers 776 (U); The Netherlands: Heyligers s.n. (U), Mennega s.n. (U), Neuman s.n. (U), Fresh Material Van der Burgh Anno 1964, idem Punt Anno 1958.
- Rumex acetosella* L. — Austria: Traxler U 49 (U); England: Gerrans 1716 (BM); Germany: Den Nijs 508-11 (AMD); France: Den Nijs 106-12 (AMD), Den Nijs 121-18 (AMD), Den Nijs 145-44 (AMD), Den Nijs 100-66 (AMD); Iceland: Ferman and Hille 48 (U), Oosterveld 0.15-76 (U), White s.n. (U); The Netherlands: Den Nijs 107-26 (AMD), De Fouw s.n., Mennega s.n. (U), Sipman 834 (U), Van der Linde-Brujnooge s.n. (U), Fresh Material Punt Anno 1954, idem Anno 1961.
- Rumex alpestris* Jacquin — France: Exc. Biol. Stud. Utrecht 1947-805 (U), Exc. Biol. Stud. Utrecht 1961-1651 (U), Guinet s.n. (MPU); Switzerland: Behrendsen s.n. (U), Kintschi 719 (U).
- Rumex aquaticus* L. — Germany: Miquel s.n. (U), s.c. s.n. Herb. U (U); The Netherlands: Buysman 1408 (U).
- Rumex bucephalophorus* L. — France: Ten Berge s.n. (U); The Netherlands: Cult. Hort. Utrecht 1972-2066 (U).
- Rumex conglomeratus* Murray — France: Exc. Biol. Stud. Utrecht 1961-1794 (U); Germany: Behrendsen s.n. (U), Exc. Biol. Stud. Utrecht 1973-20 (U); The Netherlands: Mennega s.n. (U), Swart 1412 (U).
- Rumex crispus* L. — Germany: Behrendsen s.n. (U), Exc. Biol. Stud. Utrecht 1973-29; The Netherlands: Mennega s.n. (U), Uittien s.n. (U).
- Rumex hydrolapathum* Hudson — Germany: Punt s.n. (U); The Netherlands: Dieleman 96 (U), Van Royen 363 (U), Fresh Material Voorrips Anno 1964.
- Rumex longifolius* Decandolle — Czechoslovakia: Blecha and Dvorak 1522 (U); England: Foggitt 1345 (BM); Norway: Exc. Biol. Stud. Utrecht 1965-2097.
- Rumex maritimus* L. — Denmark: Van Royen 2018 (U); The Netherlands: Colaris 94 (U), Hekking s.n. (U), Fresh Material Punt Anno 1963.
- Rumex obtusifolius* L. — England: Dandy 1253 (BM); France: Guinet s.n. (MPU); Germany: Behrendsen s.n. (U); The Netherlands: Van Steenis s.n. (U), s.c. s.n. Near Kampen (U), Fresh Material Punt Anno 1961; Yugoslavia: Exc. Biol. Stud. Utrecht 1968-1969.
- Rumex palustris* J.E. Smith — The Netherlands: Hekking s.n. (U), Oudemans 1123 (U).
- Rumex patientia* L. — Italy: Todaro 673 (U); The Netherlands: Exc. K.N.B.V. 1948-6307 (L).
- Rumex pulcher* L. — France: Leeuwenberg 1511 (U); Hungary: Wierzbicki s.n. (U); Italy: Exc. Biol. Stud. Utrecht 1963-202 (U), Schoenmakers 956-1716; Yugoslavia: Exc. Biol. Stud. Utrecht 1960-751 (U).
- Rumex rupestris* Le Gall — The Netherlands: Danser s.n. (L).
- Rumex sanguineus* L. — Germany: Exc. Biol. Stud. Utrecht 1973-30 (U); The Netherlands: Hekking s.n. (U), Simons 351 (U); Norway: Exc. Biol. Stud. Utrecht 1956-377.
- Rumex scutatus* L. — Austria: Kramer 1284 (U), Fresh Material Küster Anno 1982; France: Florschütz s.n. (U); Germany: Exc. Biol. Stud. Utrecht 1965-955 (U), Rutten s.n. (U); The Netherlands: Kok Ankersmit 6 (U).
- Rumex thyrsiflorus* Fingerhuth — The Netherlands: Boom 17477 (L), Jansen en Wachter 6173 (L).
- Rumex triangulivalvis* (Danser) Rechinger — The Netherlands: Bakhuizen v.d. Brink 4565 (U), Kern 4733 (L).

Key to the pollen types

- 1.a. Pollen pantoporate2
- b. Pollen 3- or 4-zonocolporate, pantocolporate or colpate3
- 2.a. Pollen coarsely reticulate
 *Polygonum persicaria* type

- b. Pollen tectate, micro-echinate
 *Koenigia islandica* type
- 3.a. Pollen 3-zonocolporate7
 b. Pollen 4-zonocolporate, pantocolporate,
 6-zonocolporate or pantocolporate4
- 4.a. Pollen 6-zonocolporate or pantocolporate,
 coarsely reticulate5
 b. Pollen 4-zonocolporate or pantocolporate,
 not reticulate6
- 5.a. Pollen 6-zonocolporate
 *Polygonum polystachyum* type
 b. Pollen pantocolporate
 *Polygonum amphibium* type
- 6.a. Endoapertures pori; pollen microreticulate
 *Rumex acetosa* type
 b. Endoapertures colpi or an endocingulus;
 pollen tectate
 *Polygonum aviculare* type
- 7.a. Tectum a semi-tectum, reticulate or
 micro-reticulate8
 b. Tectum imperforate or with small perforations
10
- 8.a. Exine thick (> 3 µm); columellae often
 branched, branches standing in small
 groups of 3–6 units
 *Fagopyrum esculentum* type
 b. Exine relatively thin (< 2.5 µm); columellae
 unbranched9
- 9.a. Endoapertures colpi, narrow, lalongate
 *Rheum officinale* type
 b. Endoapertures pori, circular, slightly
 lalongate or lolongate
 *Rumex acetosa* type
- 10.a. Endoapertures pori; columellae branched:
 sexine 1 distinctly thickened at the
 poles *Polygonum bistorta* type
 b. Endoapertures colpi or endocinguli,
 often with a mesoaperture; columellae
 not branched at the poles11
- 11.a. Sexine distinctly thickened at the poles;
 outline in equatorial view elliptic; columellae
 at the shoulders lowest
 *Polygonum convolvulus* type
 b. Sexine slightly thickened at the
 shoulders; outline in equatorial view
 more or less rectangular; columellae
 variable in length often longest at

shoulders
 *Polygonum aviculare* type

Description of the pollen types

Fagopyrum esculentum type (Plates 1–3)

Pollen class: 3-zonocolporate.

P/E ratio: Semi-erect to erect.

Apertures: Ectoaperture — colpus, long, slit-like, sunken; margins distinct, irregular; ends acute; colpus membrane sometimes visible, often beset with coarse granules; costae ectocolpi, extending ca. 1/4 to 1/3 towards the poles. Endoaperture — colpus, because of thick sexine often indistinct; outline elongated, lalongate, sometimes slightly rhombic; margins under the ectocolpus distinct, near the ends diffuse; a mesoaperture present or absent; if present circular; costae endocolpi, most distinct under the ectocolpi.

Exine: Very thick, uniform in thickness. Sexine thicker than nexine. Sexine 1 of columellae, high, usually branched, sometimes unbranched columellae intermingled. Sexine 2 a semi-tectum. Columellae in cross-section rounded at the top.

Ornamentation: Reticulate. At high focus “mural” areas visible (Pragłowski, 1971) which represent fused apices of columellae. Under these mural areas usually five (3–6) infratectal columellae stand in groups. These groups of columellae generally have a common basal trunk, but unbranched columellae exist also. The basal trunks distinct or indistinct. Lumina variable in outline, more or less angular. In cross-section basal trunks more or less angular, single columellae more or less circular.

Outlines: Equatorial view — elliptical. Polar view — triangular, angles obtuse, apertures in the sides; colpi intruding.

Measurements: Glycerine jelly — P 28.0–73.5 µm; E 22.5–52.5 µm; P/E ratio 1.17–1.58. Exine 3–4.5 µm. Lumina 1–1.5 µm in cross-section. Silicone oil — P 28.0–51.0 µm; E 22.5–38.5 µm; P/E ratio 1.21–1.43.

	P (μm)	E (μm)	P/E ratio
	Glycerine jelly		
<i>Fagopyrum esculentum</i>	50.0–(59.5)–73.5	36.5–(43.5)–52.5	1.17–(1.38)–1.58
<i>Fagopyrum tataricum</i>	36.5–(39.5)–44.0	27.0–(29.0)–31.5	1.32–(1.35)–1.39
	Silicone oil		
<i>Fagopyrum esculentum</i>	45.0–(48.5)–51.0	35.0–(37.0)–38.5	1.21–(1.31)–1.41
<i>Fagopyrum tataricum</i>	28.0–(33.5)–36.5	22.5–(25.0)–28.5	1.25–(1.34)–1.43

Species: Fagopyrum esculentum, F. tataricum

Key to the species

- 1.a. Pollen relatively small ($P < 45 \mu\text{m}$), basal trunks indistinct*F. tataricum*
- b. Pollen relatively large ($P > 45 \mu\text{m}$), basal trunks distinct*F. esculentum*

Comments

The *Fagopyrum esculentum* type is characterized by having branched columellae in the mesocolpium as well as at the apocolpium. Additional differential characters are the very thick exine, the reticulate ornamentation and the slit-like ectocolpi with rather diffuse endocolpi.

Wodehouse (1931) described the pollen of *Fagopyrum* as having its furrow membranes conspicuously flecked with large, coarse granules. This feature was also observed in the present study, but is not consistently present probably because of the acetolysis treatment. The best differential character between *F. esculentum* and *F. tataricum* is present in the bases of the trunks. In *F. tataricum* pollen the basal trunks are indistinct, in those of *F. esculentum* these trunks are distinct.

According to Hedberg (1946) flowers of *Fagopyrum esculentum* are heterostylic. This phenomenon is probably the reason that pollen of different specimens is very variable in size. Schoch-Bodmer (1930) and Florin (1963) mention that the size of pollen in brevistylic flowers is larger than and in longistylic flowers. The measurements given in the present study are probably from brevistylic flowers only. As the feature of heterostyly is rather

difficult to observe in dry material, no further attempt has been undertaken to study the difference in size of the pollen grains of heterostylic material.

Erdtman (1961) described *Fagopyrum esculentum* pollen as having a pitted tectum with a single columella under each pit. Praglowski (1971) gives a more extensive description of the complicated exine structures in *Fagopyrum esculentum* pollen. He stated that its pollen is subtectate, having a discontinuous tectum with slightly conical holes. The proximal ends of the columellae are frequently united to a common basal trunk, situated beneath the tectal hole. This detailed description is fully confirmed in the present study.

Pollen of *Fagopyrum* species is more or less similar to that of the *Polygonum bistorta* type. Both types are large in size, semi-erect to erect and have a thick exine which consists of branched columellae. In the *Polygonum bistorta* type these branched columellae are, however, restricted to the apocolpium and part of the mesocolpium. The latter type also shows a distinct difference in exine thickness between apocolpium and mesocolpium, whereas in the *Fagopyrum esculentum* type the exine is uniformly thick throughout.

Koenigia islandica type (Plate 4)

Pollen class: pantoporate.

Shape: Spheroidal, or slightly polygonal.

Apertures: Ectoaperture — indistinct, sometimes closed porus, variable in outline, more or less circular or slightly elongated, not or slightly depressed; margins distinct, but ir-

regular; porus membrane rarely visible, without operculum or annulus; number of pori 9–15. Endoaperture — porus, more or less circular, following the outline of the ectoporus; margins indistinct; costae absent.

Exine: Thin, equal in thickness. Sexine thicker than nexine. Sexine 1 of columellae, just visible, very low. Sexine 2 a tectum. Sexine 3 of microechinae; elements higher than basal diameter.

Ornamentation: Tectate, micro-echinate; i.e. spines $< 1 \mu\text{m}$. Columellae rather indistinct, in cross-section more or less circular in outline.

Outlines: Circular to slightly polygonal.

Measurements: Glycerine jelly — Diameter 18.5–(22.5)–27.5 μm ; Exine 1.0–1.5 μm thick. Silicone oil — Diameter 20.0–(22.0)–23.5 μm .

Species: *Koenigia islandica*

Comments

The *Koenigia islandica* type is characterized by being pantoporate and having a tectate, micro-echinate ornamentation. This combination of characters is unique in the Polygonaceae of NW Europe.

Hedberg (1946) gave a description of a *Koenigia*-type in which he not only included species of *Koenigia* but also a few species of *Polygonum*, including *P. cynaeri*, *P. filicaulis*. Some other taxa mentioned by Hedberg have colpi rather than pori and we have excluded them (e.g. *P. nummulariifolius*, *P. delicatulum*). It is clear, however, that pollen of all these taxa are morphologically related. For further taxonomic comment see Hedberg (1946). Hedberg also suggested that the pori are arranged along the edges of a cube. This may be true for the material from China that Hedberg studied, but plants from Europe and Greenland have pollen with the pores irregularly placed.

Pollen of *Koenigia* has been identified from the late Weichselian in England (Godwin, 1975) and is reported from the Late-glacial and Preboreal of Sweden (Florin, 1963).

***Polygonum amphibium* type** (Plates 5,6, fig.1)

Pollen class: Pantocolpate.

Shape: Spheroidal to ellipsoidal.

Apertures: Ecotaperture — colpus, short, narrow, not sunken; margins distinct, but irregular; ends subacute; colpi orientated as the sides of a regular pentagon; margo and costae absent; number of ectocolpi 15–27. Endoaperture — colpus, indistinct; outline following that of the ectoaperture.

Exine: Very thick. Sexine thicker than nexine. Sexine 1 of columellae of two different sizes, those of the muri of the reticulum high and distinct, those of the elements inside the lumina low. Sexine 2 a semitectum. In cross-section muri of the reticulum at the top subacute or obtuse, the elements inside the lumina rounded at the top.

Ornamentation: Coarsely reticulate. Muri duplicolumellate; the pairs of columellae forming the muri usually opposite, sometimes alternate; lumina variable in outline, but usually rectangular; granules inside the lumina distinctly visible, crowded, but limited in number, usually less than 10; in cross-section columellae either angular or more or less circular in outline; granules more or less angular in outline.

Outline: circular to elliptic.

Measurements: Glycerine jelly — Diameter 51.0–(57.0)–66.5 μm . Exine 4–5 μm thick. Granules ca. 1 μm or smaller. Silicone oil — Diameter 43.0–(46.0)–50.0 μm .

Species: *Polygonum amphibium*

Comments

The *Polygonum amphibium* type is characterized by the arrangement of its colpi in regular pentagons, and by the coarse reticulate ornamentation. This ornamentation closely resembles that of the *Polygonum persicaria* and *Polygonum polystachyum* types. The *Polygonum persicaria* type is, however, pantoporate and the *Polygonum polystachyum* type 6-zonocolpate.

Wodehouse (1931) suggested that the colpi of the *Polygonum amphibium* type are arranged as the sides of a "pentagonal dodecahedron" He called this arrangement the trischistoclastic system. In this system the *Polygonum amphibium* type would have a fixed number

of 30 colpi. It appears, however, that the number of colpi is always less than 30, perhaps because they are sometimes not regularly arranged.

Hedberg (1946) considered *Polygonum amphibium* to be a slightly aberrant variation of his *Persicaria* type. Following Wodehouse (1931) he stated: "rugae (colpi) arranged as the edges of a pentagonal dodecahedron. Reticulum more delicate than in the main type". We could see no difference between the ornamentation of the *Polygonum amphibium* type and the *Polygonum persicaria* type.

Nowicke and Skvarla (1977) consider the form of the reticulum in *Polygonum amphibium* to be unusual: "the muri are formed by distal fusion along the midline of two rows of columellae, which are opposite or sometimes alternate". They described the lumina as filled with small, free columellae. The description of the formation of the reticulum by these authors is also valid for the *Polygonum persicaria* and the *Polygonum polystachyum* types. As the shape and length of the elements inside the lumina is highly variable, these elements are called granules, although some of them may be elongated and bacula-like.

***Polygonum aviculare* type** (Plate 6, figs.2-6 to Plate 11, figs. 1-5)

Pollen class: 3-zonocolporate, 4-pantocolporate, sometimes 4-loxocolporate, or 6-12 pantocolporate.

P/E ratio: semi-erect to erect.

Apertures: Ectoaperture — colpus, long or rather long, slit-like, distinctly sunken; margins distinct, irregular; ends acute to slightly obtuse; costae ectocolpi extending 1/2 to 3/4 the length of the endoaperture towards the poles. If pantocolporate, colpi often continuous, anastomosing near the poles. Endoaperture — colpus, lalongate or a narrow endocingulus; a circular mesoaperture usually present; widest part of the endoaperture near the ectocolpus, tapering, ends diffuse; costae endocolpi or costae endocingulus most distinct around the mesoaperture.

Exine: Thick. Nexine thicker than sexine in mesocolpium or about as thick, but often thinner than sexine at the apocolpium and shoulders. Sexine 1 of columellae, distinct or indistinct, variable in length, often longest at shoulders. Sexine 2 a tectum. Sexine 3 of scabrae (only visible in SEM).

Ornamentation: Psilate. Tectum with very small perforations (puncta), only visible in SEM. Columellae in cross-section circular, small, usually more dense and smaller in mesocolpium.

Outlines: Equatorial view — slightly rectangular. Polar view — 3-colporate pollen grains circular or triangular, angles obtuse, apertures in the convex sides; pantoporate pollen circular-angular, colpi distinctly intruding, variable in length.

Measurements: Glycerine jelly — P 22.0-39.0 µm; E 17.5-32.0 µm; P/E ratio 1.16-1.49. Exine ca. 2 µm thick. Silicone oil — P 20.0-33.0 µm; E 17.0-26.0 µm; P/E ratio 1.08-1.40.

	P (µm)	E (µm)	P/E ratio
	Glycerine jelly		
<i>Polygonum arenastrum</i>	27.0-(30.5)-33.5	21.5-(23.0)-26.0	1.22-(1.34)-1.44
<i>P. aviculare</i>	31.5-(33.0)-34.5	22.0-(23.5)-25.0	1.30-(1.40)-1.49
<i>P. boreale</i>	29.0-(30.5)-31.5	23.0-(24.5)-27.5	1.21-(1.26)-1.29
<i>P. maritimum</i>	22.0-(25.5)-30.0	17.5-(19.5)-22.5	1.24-(1.19)-1.47
<i>P. oxyspermum</i>			
<i>ssp. oxyspermum</i>	28.5-(29.5)-32.5	22.5-(24.0)-25.0	1.16-(1.23)-1.30
<i>ssp. raii</i>	Diameter 23.0-(29.5)-31.0		
<i>P. patulum</i>	27.5-(33.0)-39.0	21.5-(25.5)-32.0	1.21-(1.26)-1.29
<i>P. rurivagum</i>	25.0-(29.5)-34.0	19.5-(22.5)-24.5	1.24-(1.31)-1.49

(Table continued)

	P (μm)	E (μm)	P/E ratio
	Silicone oil		
<i>Polygonum arenastrum</i>	26.0-(29.5)-32.0	21.0-(23.0)-26.0	1.15-(1.27)-1.38
<i>P. aviculare</i>	20.0-(26.5)-33.0	17.0-(21.0)-26.0	1.11-(1.24)-1.40
<i>P. boreale</i>	25.0-(27.5)-31.0	19.5-(23.0)-25.0	1.08-(1.19)-1.30
<i>P. maritimum</i>	20.0-(23.0)-25.0	17.0-(18.5)-19.5	1.12-(1.22)-1.35
<i>P. oxyspermum</i>			
<i>ssp. oxyspermum</i>	28.0-(30.0)-32.0	22.5-(25.0)-26.0	1.11-(1.22)-1.35
<i>ssp. raii</i>	Diameter 25.0-(28.0)-31.0		
<i>P. patulum</i>	23.5-(26.0)-27.0	19.5-(21.0)-23.0	1.17-(1.22)-1.28
<i>P. rurivagum</i>	22.5-(25.5)-28.5	18.0-(19.5)-22.5	1.13-(1.25)-1.31

Species: *Polygonum arenastrum*, *P. aviculare*,
P. boreale, *P. maritimum*, *P. oxyspermum*, *P.*
patulum, *P. rurivagum*

TABLE I

Proportion of tricolporate grains (%)

<i>P. arenastrum</i>		<i>P. oxyspermum</i> ssp. <i>oxyspermum</i>	
Exc. Stud. Biol. 1964-635	99	Fries 668	72
Exc. Stud. Biol. 1966-1623	100	<i>P. oxyspermum</i> ssp. <i>raii</i>	
Hessel 1242	100	Alm 54	13
Unar 1525	100	Nannfeldt s.n.	8
<i>P. aviculare</i>		Samuelsson s.n.	9
Hekking s.n.	96	<i>P. patulum</i>	
Küster s.n.	100	Bakhuizen v.d.Brink 5390	77
Punt, fresh Material	99	Sutter v.L. 425	99
Swart 259	92	<i>P. rurivagum</i>	
Wilmott 534B	99	Clermont et Rione s.n.	51
Wilson 36	85	Héribaud-Joseph s.n.	55
<i>P. boreale</i>		Hessel, Klein and Rubers 2206	71
Allerton Gray School 54	75		
Jahlsberg s.n.	42		

Key to the groups

- 1.a. Sexine in mesocolpium thinner than nexine; sexine in apocolpium not or only slightly thicker than elsewhere; columellae relatively low and indistinct
..... *P. oxyspermum* group
(Species: *P. maritimum*, *P. oxyspermum*)
- b. Sexine in mesocolpium thicker than nexine; sexine distinctly thicker towards the shoulders and at the apocolpium; columellae relatively high and distinct
..... *P. aviculare* group
(Species: *P. arenastrum*, *P. aviculare*, *P.*
boreale, *P. patulum*, *P. rurivagum*)

Comments

The *Polygonum aviculare* type is characterized by its thick nexine, imperforate tectum, rectangular outline in equatorial view and lalongate, tapering endocolpi, which are sometimes elongated into an endocingulus.

The two groups distinguished are mainly separated on the length of the columellae at the apocolpium. A further differentiation on the basis of aperture number, as proposed by Hedberg (1946), is not used here, since 4-aperturate pollen grains occur in all predominantly 3-aperturate specimens and vice-versa.

According to Hedberg (1946) many more species belong to his *Avicularia* type; they all belong to the subgenus *Avicularia*.

The *P. aviculare* type resembles the *P. convolvulus* type in some characters, but differs in having a sexine which is usually thicker at the shoulders than in the mesocolpium and apocolpium. This makes the outline more or less rectangular. Another difference is found in the endoaperture which in *P. aviculare* is usually an endocolpus and only sometimes a narrow endocingulus, whereas the endoaperture in the *P. convolvulus* type is always a distinct endocingulus. Moreover, in the SEM the surface around the ectocolpi lacks the characteristic margo of scabrae. The *P. bistorta* type is also slightly rectangular in equatorial view, and has a closed tectum, but it differs in the presence of branched columellae in the apocolpium and its larger size.

The *P. aviculare* type is remarkably variable in the number of ectoapertures. The pollen of some species is predominantly 3-colporate (e.g. *P. aviculare*, *P. maritimum*), whereas other taxa have a majority of pantocolporate grains (e.g. *P. oxyspermum* ssp. *raii*). The number of ectoapertures is often more than 6, and maybe up to 9. Some species show a mixture (e.g. *P. boreale*). If there are more than 3 ectoapertures, one or more of the endoapertures is often lacking. This unusual fact also occurs in some *Rumex* species (p.94).

The colpi in 4-colporate grains are sometimes arranged in a loxocolporate fashion (Erdtman, 1952) while in other grains the ectocolpi are so elongated that they anastomose at the poles.

***Polygonum bistorta* type** (Plate 11, figs.6–7 to Plate 15, figs.1–3)

Pollen class: 3-zonocolporate, rarely 4-loxocolporate.

P/E ratio: semi-erect to erect.

Apertures: Ectoaperture — colpus, rather long, slit-like, sunken; margins distinct, irregular; ends acute; colpus membrane not visible; costae ectocolpi extending from equator to ca. 1/2 or 3/4 towards the poles. Endoaperture — porus, circular or lalongate; rarely with small horns; costae endopori, most distinct near ectocolpus; ends diffuse.

Exine: Thick to very thick, thickest in apocolpium. Sexine distinctly thicker than nexine. Sexine 1 of columellae, distinct, dense, longest at poles, branched in upper part of mesocolpium and at apocolpium. Sexine 2 a tectum, uniform in thickness. Sexine 3 of small scabrae only visible in SEM.

Ornamentation: Psilate. Small perforations (puncta) in tectum largest at apocolpium. Columellae in cross-section circular to angular.

Outlines: Equatorial view — elliptic to slightly rectangular. Polar view — triangular, angles obtuse, apertures in convex sides. Colpi distinctly intruding.

Measurements: Glycerine jelly — P 33.0–76.0 µm; E 27.0–60.0 µm; P/E ratio 1.13–1.38. Exine variable in thickness; in mesocolpium 2–4 µm; at apocolpium 4–6 µm. Silicone oil — P 33.0–53.0 µm; E 27.0–41 µm; P/E ratio 1.18–1.42.

Species: *Polygonum amplexicaule*, *P. bistorta*, *P. viviparum*

	P (µm)	E (µm)	P/E ratio
	Glycerine jelly		
<i>P. amplexicaule</i>	33.0–(35.0)–37.5	27.0–(29.0)–30.5	1.13–(1.22)–1.29
<i>P. bistorta</i>	49.5–(58.5)–68.5	37.5–(44.5)–50.5	1.24–(1.31)–1.38
<i>P. viviparum</i>	47.5–(55.0)–76.0	36.0–(43.5)–60.0	1.16–(1.28)–1.37
	Silicone oil		
<i>P. amplexicaule</i>	33.0–(35.0)–37.0	27.0–(28.5)–30.5	1.19–(1.23)–1.29
<i>P. bistorta</i>	39.5–(48.0)–53.0	31.5–(35.0)–37.5	1.25–(1.37)–1.42
<i>P. viviparum</i>	37.0–(43.5)–51.0	29.0–(34.5)–41.0	1.18–(1.26)–1.34

Key to the species

- 1.a. Sexine not conspicuously increasing in size towards apocolpium, at poles at least 3 μm thick, usually more; grains large, usually < 38 μm *P. amplexicaule*
- b. Sexine increasing towards apocolpium, but not conspicuously so, at poles no thicker than 2.5 μm ; grains very large, > 38 μm 2
- 2.a. Channels between columellae at apocolpium more or less regular in width, narrow, no wider than columella breadth; branched columellae extending no more than halfway down grains from poles *P. viviparum*
- b. Channels between columellae at apocolpium irregular in width, often broader than columella diameter; branched columellae often extending from poles almost to equator *P. bistorta*

Comments

The *P. bistorta* type is characterized by its very variable columellae. The columellae in the equatorial plane are usually simple, relatively short and crowded, but they increase considerably in length towards the apocolpium where they are branched, coarse and more or less spread out widely. In *P. bistorta*, small branched columellae may even occur at the equator and are certainly present just above it, whereas in *P. viviparum* branched columellae extend no further than halfway down the mesocolpium from the poles.

Another character of importance is the spacing between the coarse columellae. In *P. bistorta* the dividing channels are distinct, relatively broad, irregular in width and often wider than the smallest columellae. In *P. viviparum*, on the other hand, the channels are relatively narrow, less distinct and always narrower than the coarse columellae, moreover they are often regular in width (Plate 12, figs.3,4 and Plate 13, figs.3,4).

In *P. bistorta* the endoapertures in mature pollen grains are more or less circular with diffuse ends. Pollen of *P. viviparum* often tends

to have alongate endopori. This difference is, unfortunately, not consistent. All other characters of both taxa are remarkably similar, especially those of the surface, so SEM-micrographs are of little help in the separation of the two species. Sometimes endoapertures are lacking; such aberrant pollen is especially characteristic of arctic samples (Van der Knaap, pers. comm., 1986).

The *P. bistorta* type resembles the *Fagopyrum esculentum* type in their ectocolpi, size, P/E ratio and, more or less, in their endoapertures. They both have branched columellae, but in *Polygonum bistorta* these are restricted to the apocolpium and part of the mesocolpium, although right down to the equator in *P. bistorta*. In the *Fagopyrum esculentum* type all the columellae are branched.

Palynologists generally take the view that it is impossible to distinguish pollen of *P. viviparum* from that of *P. bistorta* (Florin, 1969; Godwin, 1975). We believe that the characters given in the "key to the species" above are effective in separating the majority of grains.

This well defined pollen type has been found in a number of species which all belong to Section *Bistorta* Meissner (Hedberg, 1946) and Hedberg called it the *Bistorta* type. For this reason we have retained the name *bistorta* for the group. According to Nowicke and Skvarla (1977) the densely packed columellae, in the mesocolpial area, which are visible in their TEM- and LM-micrographs, are a unique feature not present in any of the other taxa of Polygonaceae they investigated.

P. amplexicaule is an East-Asian species, but has become naturalized in England and Ireland (Jalas and Suominen, 1979).

***Polygonum convolvulus* type** (Plate 15 figs.4-7 and Plate 16)

Pollen class: 3-zonocolporate.

P/E ratio: semi-erect to erect, sometimes adequate to suberect.

Apertures: Ectoaperture — colpus, rather long, narrow, slit-like, not particularly sunken; margins distinct, irregular; ends acute to slightly obtuse; colpus membrane not visible; costae

ectocolpi extending from equator about half-way to the poles; in SEM distinct margo of scabrae in a broad area around ectocolpus. Endoaperture — endocingulus, slightly tapering towards mesocolpium; margins distinct; mesoaperture present, circular in outline; costae on both sides of endocingulus, thickest at mesoaperture.

Exine: Thick. Sexine thicker than nexine. Sexine 1 of columellae, distinct, longer in mesocolpium and at poles than at shoulders. Sexine 2 a tectum, thin, distinctly thickened in centre of mesocolpium and at poles. Sexine 3 of scabrae, scarce in mesocolpium and at poles (SEM), absent elsewhere.

Ornamentation: Psilate, punctate in mesocolpium, scabrate around ectocolpi. Columellae in cross-section more or less circular, sometimes angular. In mesocolpium columellae denser and smaller.

Outlines: Equatorial view — elliptical, rarely circular. Polar view — either hexagonal or triangular, rarely circular; angles obtuse, sides convex and apertures in obtuse angles; colpi intruding.

Measurements: Glycerine jelly — P 28.0–34.0 μm ; E 22.5–29.5 μm ; P/E ratio 1.00–1.43. Exine at poles 2–3.5 μm , at shoulders 1–2.5 μm . Silicone oil — 24.5–29.5 μm ; E 19.0–22.0 μm ; P/E ratio 1.16–1.35.

Pollen grains of this type resemble those of the *P. aviculare* type in many characters, but differ mainly in their elliptical outline in equatorial view and the distinctly elongated columellae at the poles.

We were not able to differentiate the pollen of the two taxa in the type although Hedberg (1946) indicated differences in colpus length and surface structures. According to our own observations, the length of the colpus is too variable to separate them reliably and the features of the ornamentation were identical in our material.

Nowicke and Skvarla (1977) described the ornamentation of the margo around the ectocolpus as being echinate. As the elements are smaller than 1 μm , and only visible in SEM, it seems better to describe them as scabrae.

Polygonum persicaria type (Plates 17–23)

Pollen class: Pantoporate.

Shape: Spheroidal to ellipsoidal.

Apertures Ectoaperture — porus, circular, situated in a single lumen of the reticulum, not sunken: margins not particularly distinct; number of pori 12–27. Endoaperture — porus, slightly smaller than ectoaperture; margin distinct, irregular; no costae.

Exine: Thick to very thick. Sexine much

	P (μm)	E (μm)	P/E ratio
	Glycerine jelly		
<i>Polygonum convolvulus</i>	28.0–(31.0)–34.0	22.5–(24.5)–29.5	1.00–(1.28)–1.43
<i>P. dumetorum</i>	28.0–(30.5)–34.0	22.5–(24.5)–27.0	1.14–(1.23)–1.31
	Silicone oil		
<i>P. convolvulus</i>	24.5–(26.0)–27.5	19.0–(20.5)–21.5	1.22–(1.29)–1.35
<i>P. dumetorum</i>	24.5–(27.0)–29.5	19.0–(21.0)–22.0	1.16–(1.27)–1.35

Species: *Polygonum convolvulus*, *P. dumetorum*

Comments

The *P. convolvulus* type is characterized by 3-zonocolporate pollen which has an endocingulus and a distinctly thickened sexine at the apocolpium as well as in the mesocolpium.

thicker than nexine. Sexine 1 of columellae in muri of reticulum and of spherical elements inside lumina (granules). Sexine 2 a semi-tectum. Muri in cross-section acute to rounded at apex; granules rounded at apex.

Ornamentation: Coarsely reticulate. Muri thin, duplicolumellate, columellae usually opposite,

sometimes alternate; lumina variable in size, angular, usually forming 4–6 sided polygons, the sides straight in fully expanded grains, slightly wavy in contracted grains (harmomegathy); granules numerous inside lumina, isodiametric in outline. In cross-section columellae circular to rectangular.

Outlines: Circular to elliptic.

Measurements: Glycerine jelly — Diameter 32.5–55 µm. Exine 3–6 µm thick. Silicone oil — Diameter 28–50.0 µm.

	Diameter (µm)
	Glycerine jelly
<i>Polygonum foliosum</i>	32.5–(36.5)–41.0
<i>P. hydropiper</i>	42.5–(49.0)–55.0
<i>P. lapathifolium</i>	33.5–(36.5)–40.0
<i>P. minus</i>	40.5–(45.0)–55.0
<i>P. mite</i>	46.0–(50.0)–52.0
<i>P. persicaria</i>	41.5–(48.0)–52.0
	Silicone oil
<i>P. foliosum</i>	32.0–(34.5)–36.5
<i>P. hydropiper</i>	41.5–(44.5)–50.0
<i>P. lapathifolium</i>	28.0–(32.0)–35.0
<i>P. minus</i>	35.0–(39.5)–42.0
<i>P. mite</i>	38.0–(42.5)–45.5
<i>P. persicaria</i>	31.5–(39.5)–46.5

Species: *Polygonum foliosum*, *P. hydropiper*, *P. lapathifolium*, *P. minus*, *P. mite*, *P. persicaria*

Key to the species

- 1.a. Lumina with pori larger than lumina without pori*P. foliosum*
- b. Lumina with pori smaller than lumina without pori*P. persicaria* group
(Species: *P. hydropiper*, *P. lapathifolium*, *P. minus*, *P. mite*, *P. persicaria*)

Comments

The *P. persicaria* type is easily recognized by its large number of pores (pantoporate) and characteristic coarse reticulum with duplicolumellate muri. A similar reticulum is seen in the *P. polystachyum* type and the *P. amphibium*

type, but both these types differ in their apertures. The former is 6-zonocolpate whereas the latter is pantocolpate.

P. foliosum pollen is separated on the basis of the diameter of porus lumina. Although the diameter of the lumina with pores is variable, in *P. foliosum* these lumina are always larger than those of the surrounding reticulum. In all other species of *Polygonum* that we have examined, the lumina with pores are smaller than those of the surrounding reticulum. A further separation of the taxa into groups or species was not possible; the grains of this type are extremely similar. There is some variation in the shape and height of the muri. In some of them the tips of the columellae, which form the muri are obtuse in cross-section (*P. lapathifolium*), others are more sharply edged (*P. minus*). The length of the columellae may be relatively short (e.g. *P. lapathifolium*) or relatively long (e.g. *P. minus*, *P. mite* and *P. persicaria*). But the overlap is so large that we could not rely on these characters to create smaller groups or to distinguish species.

Wodehouse (1931) suggested that the pores in his *Persicaria* section are arranged according to the trischistoclastic system. In this arrangement, the pores are situated in the middle of the sides of the pentagons on the face of a pentagonal dodecahedron. If this system is perfect all pollen grains should have 30 pores. Hedberg (1946) disagreed with Wodehouse and mentioned that it seems, that pores in his *Persicaria* type are more disorderly arranged. The pollen grains we studied have less than 30 pores. In fact the variation in pore-number is great, even within one taxon they may range from 12–27 pores. Maybe the saving of apertures conforms to an ideal, which perfectly-formed grains fit, although the development of most grains introduces variations.

Polygonum polystachyum type (Plate 24)

Pollen class: 6-Zonocolpate.

P/E ratio: Subtransverse, adequate or suberect.
Apertures: Ectoaperture — colpus, long, narrow, not sunken; margins distinct, irregular;

ends acute. Endoaperture — congruent with ectoaperture or absent.

Exine: Thick. Sexine thicker than nexine. Sexine 1 of columellae in muri of reticulum and of granules inside lumina. Sexine 2 a semi-TECTUM. Muri in cross-section rounded at apex; thicker than granules.

Ornamentation: Coarsely reticulate. Muri thin, straight or slightly wavy depending on degree of expansion (see under *P. persicaria* type, p.11); duplicolumellate, columellae forming muri usually opposite, sometimes alternate. Lumina variable in size and outline, usually 4–6 sided. Columellae circular to rectangular in outline.

Outlines: Equatorial view — circular to elliptic. Polar view — circular; colpi intruding.

Measurements: Glycerine jelly — P 24.5–(29.5)–33.5 µm; E 27.0–(31.0)–34.5 µm; P/E ratio 0.91–(0.96)–1.04. Exine 2.0–3.0 µm. Silicone oil — P 23.0–(28.0)–35.0 µm; E 26.0–(29.5)–34.5 µm; P/E ratio 0.85–(0.93)–1.03.

Species: *Polygonum polystachyum*

Comments

The *P. polystachyum* type is characterized by being 6-zonocolpate and having a coarse, reticulate ornamentation with duplicolumellate muri. This ornamentation is similar to that of the *P. persicaria* and *P. amphibium* types, but these differ in their apertural system. The *P. persicaria* type is pantoporate and the *P. amphibium* type pantocolpate.

Hedberg (1946) included *P. polystachyum* in his *Aconogonon* type. This type, however, is 3-colporate and from his figs.25–27 (examples of the *Aconogonon* type) it is clear that in this type pollen is basically tectate. Hedberg's material was probably misidentified.

P. polystachyum was originally from the Himalayas (Tutin, 1964), but since it is naturalized in N.W. Europe it has been included here.

***Rheum officinale* type** (Plates 25,26, figs.1–3)

Pollen class: 3-Zonocolporate.

P/E ratio: Semitransverse to semi-erect.

Apertures: Ectoaperture — colpus, long, slit-like, distinctly sunken; margins distinct, irregular; ends acute; colpus membrane not visible; costae ectocolpi extending from equator ca. 1/3 towards poles. Endoaperture — colpus, narrow, lalongate, tapering towards ends; margins at ends diffuse; ends subacute; costae endocolpi most distinct near ectocolpus.

Exine: Rather thin to thick, uniform in thickness. Sexine thicker than nexine. Sexine 1 of columellae, distinct, short, uniform in length. Sexine 2 a semi-TECTUM. Capita of muri circular in cross-section. Sexine 3 of scabrae, only visible in SEM.

Ornamentation: Finely reticulate or micro-reticulate. Muri usually simplicolumellate. Lumina variable in outline, more or less angular. Columellae circular in cross-section.

Outlines: Equatorial view — elliptic. Polar view — circular; colpi intruding.

Measurements: Glycerine jelly — P 28.0–(29.5)–30.5 µm; E 26.0–(26.5)–27.0 µm; P/E ratio 1.04–(1.11)–1.17. Exine 1.5–2.5 µm thick. Lumina ca. 1 µm or less in diameter. Silicone oil — P 21.5–(24.0)–27.0 µm; E 22.5–(23.5)–25.0 µm; P/E ratio 0.86–(1.02)–1.14.

Species: *Rheum officinale*

Comment

The *R. officinale* type is characterized by being 3-zonocolporate, finely reticulate, and having a small, lalongate endocolpus.

Wodehouse (1931) stated that *R. officinale* pollen grains are similar to those of *Rumex acetosella*, but that the exine is somewhat thicker and the pitting finer than in *R. acetosella*. The grains of *Rheum officinale* that we studied, are, indeed, similar in some respects to those of the *Rumex acetosella* type, but the main difference is found in the narrow, lalongate endocolpus of *Rheum officinale* pollen; *Rumex acetosella* pollen has an endoporus.

Several species of *Rheum*, a genus originally from temperate Asia, are cultivated, either as a purgative or for their edible petioles (Tutin, 1964). Because of the economic importance of this genus, pollen of one species has been included here.

***Rumex acetosa* type** (Plate 26, figs.4–8 to Plate 42)

Pollen class: 3-Zono- or (4–9) pantocolporate, rarely 4-loxocolporate.

P/E ratio: 3-Zonocolporate grains usually subtransverse, sometimes semitransverse, rarely adequate or suberect. Shape of pantoporate grains usually ellipsoidal.

Apertures: Ectoaperture — colpus, narrow, slit-like, long to very long, usually sunken, sometimes not or only slightly sunken; margins distinct, irregular; ends acute; costae ectocolpi extending from equator nearly to poles, usually rather indistinct. Endoaperture — porus; outline circular, slightly lalongate or more or less lalongate; costae endopori present, sometimes interrupted at the equator, narrow, but distinct.

Exine: Rather thick. Sexine thicker than nexine. Sexine 1 of columellae, low, either distinct

or indistinct, uniform in thickness. Sexine 3 of scabrae, visible only in SEM.

Ornamentation: Microreticulate. Muri simpli-columellate, often irregular in surface view (visible in SEM), always beset with granular scabrae (SEM). Lumina irregular in outline, usually more or less circular, sometimes indistinct. Columellae circular in cross-section.

Outlines: Equatorial view — usually elliptical, sometimes circular. Polar view — more or less circular; colpi not, slightly, or distinctly intruding.

Measurements: Glycerine jelly — P 18.0–33.0 μm ; E 17.5–37.0 μm ; P/E ratio 0.83–1.10. Diameter of pantocolporate grains up to 59.0 μm . Exine 1–2.5 μm thick. Diameter of endopori 3–5.5 μm . Silicone oil P 14.5–31.0 μm ; E 17.5–35.0 μm ; P/E ratio 0.85–1.04. Diameter of pantocolporate pollen grains up to 52.0 μm .

	P (μm)	E (μm)	P/E ratio
	Glycerine jelly		
<i>Oxyria digyna</i>	20.0–(23.0)–26.0	21.5–(23.0)–26.0	0.93–(0.99)–1.10
<i>Rumex acetosa</i>	19.0–(21.5)–25.8	20.5–(23.0)–26.0	0.85–(0.93)–0.97
<i>R. acetosella</i>			
2N=14	17.0–(18.0)–19.5	18.0–(19.0)–21.5	0.91–(0.94)–0.96
2N=28	16.5–(19.0)–20.5	17.5–(20.5)–21.5	0.91–(0.95)–0.97
2N=42	Diameter 20.0–(25.0)–27.0		
<i>R. alpestris</i>	21.0–(24.0)–27.0	23.0–(26.0)–28.0	0.83–(0.92)–0.95
<i>R. aquaticus</i>	Diameter 32.0–(38.5)–45.0 (–59.0)		
<i>R. bucephalophorus</i>	21.0–(23.0)–25.5	22.5–(24.5)–29.5	0.87–(0.94)–0.97
<i>R. conglomeratus</i>	23.0–(26.0)–28.0	24.5–(27.5)–30.0	0.88–(0.95)–1.00
<i>R. crispus</i>	27.0–(29.5)–31.0	30.0–(32.0)–34.0	0.89–(0.93)–0.97
<i>R. hydrolapathum</i>	Diameter 32.5–(40.0)–46.0		
<i>R. longifolius</i>	Diameter 32.0–(36.5)–39.0		
<i>R. maritimus</i>	24.0–(28.5)–33.0	25.5–(30.5)–37.0	0.90–(0.94)–0.99
<i>R. obtusifolius</i>	Diameter 32.0–(36.0)–40.0		
<i>R. palustris</i>	Diameter 37.5–(40.0)–42.5		
<i>R. patientia</i>	25.0–(29.0)–30.5	29.0–(31.0)–34.0	0.83–(0.93)–0.99
<i>R. pulcher</i>	23.5–(26.5)–30.0	24.0–(27.5)–30.5	0.93–(0.96)–1.00
<i>R. rupestris</i>	23.0–(24.5)–25.5	25.0–(26.5)–28.5	0.84–(0.92)–0.95
<i>R. sanguineus</i>	22.5–(26.5)–30.5	24.0–(28.0)–34.5	0.91–(0.94)–1.00
<i>R. scutatus</i>	23.0–(25.0)–26.5	24.0–(26.0)–27.5	0.89–(0.97)–1.04
<i>R. thyrsiflorus</i>	18.0–(19.5)–21.0	19.0–(21.0)–22.5	0.86–(0.93)–0.99
<i>R. triangulivalvis</i>	19.5–(22.0)–23.0	20.5–(23.0)–24.0	0.94–(0.95)–0.97
	Silicone oil		
<i>Oxyria digyna</i>	18.0–(20.0)–21.5	20.0–(21.0)–23.5	0.89–(0.94)–1.00
<i>Rumex acetosa</i>	17.0–(19.0)–21.5	18.5–(20.5)–24.0	0.87–(0.93)–0.97
<i>R. acetosella</i>			
2N=14	14.5–(16.0)–17.0	16.0–(17.5)–19.0	0.86–(0.91)–0.98
2N=28	16.5–(17.5)–19.0	17.0–(18.5)–19.5	0.91–(0.94)–0.97
2N=42	Diameter 19.0–(22.5)–25.0		

(Table continued)

	P (μm)	E (μm)	P/E ratio
<i>R. alpestris</i>	19.5-(21.0)-23.0	21.5-(23.0)-25.0	0.87-(0.91)-0.96
<i>R. aquaticus</i>	Diameter 31.0-(32.5)-36.0 (-52.0)		
<i>R. bucephalophorus</i>	19.0-(21.5)-23.0	20.5-(23.0)-24.5	0.87-(0.94)-0.97
<i>R. conglomeratus</i>	21.0-(23.0)-24.5	21.5-(24.5)-27.5	0.86-(0.93)-0.97
<i>R. crispus</i>	25.0-(28.5)-33.0	28.0-(31.5)-35.0	0.87-(0.92)-0.97
<i>R. hydrolapathum</i>	Diameter 33.0-(40.0)-46.0		
<i>R. longifolius</i>	Diameter 32.0-(33.5)-35.0		
<i>R. maritimus</i>	25.5-(28.0)-31.5	26.0-(29.0)-32.5	0.92-(0.97)-1.00
<i>R. obtusifolius</i>	Diameter 27.5-(33.5)-35.0		
<i>R. palustris</i>	Diameter 27.5-(31.5)-32.0		
<i>R. patientia</i>	22.5-(26.0)-27.0	24.0-(28.0)-29.5	0.85-(0.92)-0.97
<i>R. pulcher</i>	23.0-(26.0)-28.5	23.5-(27.5)-29.0	0.92-(0.95)-0.99
<i>R. rupestris</i>	21.5-(23.0)-24.0	23.0-(25.0)-26.0	0.91-(0.92)-0.95
<i>R. sanguineus</i>	19.0-(23.0)-25.5	22.0-(25.5)-28.0	0.87-(0.91)-0.93
<i>R. scutatus</i>	20.5-(22.5)-24.5	20.5-(23.0)-25.5	0.89-(0.97)-1.04
<i>R. thysiflorus</i>	16.0-(17.5)-19.5	18.0-(19.0)-20.0	0.89-(0.92)-0.97
<i>R. triangulivalvis</i>	18.5-(20.0)-21.0	20.0-(21.5)-23.5	0.86-(0.93)-0.96

Species: *Oxyria digyna*, *Rumex acetosa*, *R. acetosella*, *R. alpestris*, *R. aquaticus*, *R. bucephalophorus*, *R. conglomeratus*, *R. crispus*, *R. hydrolapathum*, *R. longifolius*, *R. maritimus*, *R. palustris*, *R. patientia*, *R. pulcher*, *R. rupestris*, *R. sanguineus*, *R. scutatus*, *R. thysiflorus*, *R. triangulivalvis*

TABLE II

Proportion of 3-colporate grains (%)

<i>Oxyria digyna</i>	100	<i>R. hydrolapathum</i>	
<i>Rumex acetosa</i>		Dieleman 96	1
Hessel, Klein and Rubers 776	82	Punt s.n.	1
Krüger and Bick H.J. 114	94	<i>R. longifolius</i>	
Neuman s.n.	83	Foggitt 1345	0
Punt, fresh material	12	Exc. Stud. Biol. 1961-2097	15
<i>R. acetosella</i>		<i>R. maritimus</i>	100
Den Nijs 106-12 (2N=14)	96	<i>R. obtusifolius</i>	
Den Nijs 121-18 (2N=14)	80	Behrendsen s.n.	1
Den Nijs 145-44 (2N=28)	82	Hort. Bot. Utrecht s.n.	0
Den Nijs 508-11 (2N=28)	70	Van Steenis s.n.	0
Den Nijs 7-26 (2N=42)	2	<i>R. palustris</i>	
Den Nijs 100-66 (2N=42)	14	Hekking s.n.	1
De Fouw s.n.	60	Herb. Oudemans 1123	1
Ferman and Hille 48	56	<i>R. patientia</i>	
Gerrans 1716	1	Bot. Exc. K.N.B.V. 6307	30
Oosterveld O.15-76	36	Todaro 673	27
Punt, fresh material	18	<i>R. pulcher</i>	
Van der Linde-Brujnooge s.n.	52	Exc. Stud. Biol. 1963-202	99
White s.n.	10	Leeuwenberg 1511	99
<i>R. alpestris</i>		Wierzbicki s.n.	99
Behrendsen s.n.	45	<i>R. rupestris</i>	
Exc. Stud. Biol. 1947-805	20	Danser s.n.	99
Kintschi 719	12	<i>R. sanguineus</i>	99
<i>R. aquaticus</i>	0	<i>R. scutatus</i>	100

TABLE II (continued)

<i>R. bucephalophorus</i>		<i>R. thyrsiflorus</i>	
Cult. Hort. Utrecht 1972-2066	100	Boom 17477	95
Ten Berge s.n.	88	Jansen en Wachter 6173	82
<i>R. conglomeratus</i>	100	<i>R. triangulivalvis</i>	
<i>R. crispus</i>		Kern 4733	97
Behrendsen s.n.	84		
Exc. Stud. Biol. 1973-29	10		
Mennega s.n.	65		
Uittien s.n.	56		

Key to species and groups

- 1.a. Ectocolpi 3; pollen zonocolporate 2
 b. Ectocolpi 4 or more; pollen panto-or loxocolporate 9
- 2.a. Ectocolpi not or only slightly intruding in polar view, outline more or less circular 3
 b. Ectocolpi intruding in polar view, outline lobed 6
- 3.a. Endopori more or less lalongate 4
 b. Endopori circular 5
- 4.a. Costae endopori narrow, hardly visible, sometimes interrupted; colpi not particularly long; apocolpium large
R. alpestris
 b. Costae endopori distinct, not interrupted; colpi long; apocolpium of medium size *R. triangulivalvis*
- 5.a. Pollen large ($E > 26 \mu\text{m}$); columellae distinct in cross-section; colpi usually slightly intruding *R. crispus* (p.p.)
 b. Pollen rather small ($E < 26 \mu\text{m}$); columellae indistinct in cross-section
R. acetosa group
 (Species: *R. acetosa*, *R. thyrsiflorus*)
- 6.a. Grains rather small ($E < 26 \mu\text{m}$); endopori circular or lalongate; costae endopori either interrupted or complete8
 b. Grains large ($E > 26 \mu\text{m}$); endopori circular or lalongate; costae endopori distinct and usually complete7
- 7.a. Endopori circular
R. sanguineus group
 (Species: *R. bucephalophorus*, *R. rupestris*, *R. sanguineus*, *R. crispus* (p.p.)
- b. Endopori lalongate
R. conglomeratus group
 (Species: *R. conglomeratus*, *R. maritimus*, *R. pulcher*, *R. scutatus*)
- 8.a. Endopori usually distinctly interrupted, often lalongate; reticulum indistinct, columellae faint *R. acetosella*
 b. Endopori usually complete, circular; reticulum more or less distinct, columellae distinct *Oxyria digyna*
- 9.a. Endopori circular or slightly lalongate 10
 b. Endopori more or less lalongate 13
- 10.a. Costae endopori indistinct, often interrupted, pollen rather small ($E < 26 \mu\text{m}$); reticulum usually indistinct 11
 b. Costae endopori distinct, pollen large ($E > 26 \mu\text{m}$); reticulum usually distinct 12
- 11.a. Ectocolpi long, distinctly sunken (intruding); apocolpium index small (< 0.30)
R. acetosella
 b. Ectocolpi relatively short, not or only very slightly sunken; apocolpium index medium or large (> 0.30)
R. acetosa group
 (Species: *R. acetosa*, *R. thyrsiflorus*)
- 12.a. Pollen very large, ca. $40 \mu\text{m}$ or larger; sexine surface often very irregular
R. aquaticus group
 (Species: *R. aquaticus*, *R. hydrolapathum*)
 b. Pollen large, usually between 30 and $40 \mu\text{m}$, sexine surface smooth
R. palustris group
 (Species: *R. palustris*, *R. patientia* (p.p.), *R. crispus* (p.p.)

- 13.a. Ectocolpi not particularly long, not sunken (not intruding), costae endopori very narrow, often indistinct, sometimes interrupted; pollen relatively small, $D < 26 \mu\text{m}$ *R. alpestris*
- b. Ectocolpi long, sunken (intruding), costae endopori distinct, usually complete; pollen large, $D > 26 \mu\text{m}$
 *R. obtusifolius* group
 (Species: *R. longifolius*, *R. obtusifolius*,
R. patientia (p.p.), *R. crispus* (rarely))

Comments

Pollen grains of the *Rumex acetosa* type are easily recognized by their fine reticulum, very narrow, slit-like ectocolpus and more or less circular, small endoporus with narrow costae. The only pollen type in the European Polygonaceae that resembles is the *Rheum officinale* type, but in that type the reticulum is more distinct (larger lumina) and the endoaperture is a colpus.

Although the pollen of *Rumex* species are very similar; it is possible to recognize distinct pollen groups, and sometimes even species. Features used for the identification of pollen in *Rumex* are:

(I) Number of colpi

Some species often are predominantly 3-colporate (e.g. *R. maritimus*, *R. sanguineus*), whereas others have a majority of 4–9-colporate grains (e.g. *R. aquaticus*, *R. obtusifolius*). Several species, however, show a mixture of 3-colporate and 4–9-colporate grains (e.g. *R. acetosa*, *R. crispus*). Table II gives a survey of the proportions of 3-colporate pollen present in the specimens of all *Rumex* species we examined. Species with a mixture of colpus numbers often exhibit a wide range of percentages. In *R. acetosella*, a taxon with 3 different cytotypes (14, 28 and 42 chromosomes), the number of colpi varies significantly with the ploidy level. After a thorough study of material from Europe, Den Nijs et al. (1980) could draw 3 main conclusions:

(1) Diploids always have a very high proportion of 3-colporate pollen grains, but even in these diploids there are a certain number of

pantoporate grains: in one specimen the figure was up to 20%.

(2) At the tetraploid level the proportion of 3-colporate pollen varies from 56 to 100%. Even in populations from a single site there is a striking heterogeneity in this feature.

(3) At the hexaploid level the range of variation is still wider giving figures between 1 and 99% 3-colporate pollen. Specimens in which low percentages of 3-colporate pollen are present, occur especially in Western Europe and are less frequent elsewhere.

From the combined results of Den Nijs and of the present study, it is clear that relatively few specimens of *Rumex* species are either exclusively 3-colporate or pantocolporate.

(II) Length of colpi

The length of the colpi is of great significance in *Rumex* pollen. Andersen (1961) and subsequently Moore and Webb (1978) have laid special emphasis on the difference in length of the colpi between *R. acetosa* and *R. acetosella* pollen. They recognize pollen of *R. acetosa* by its relatively short colpus, whereas *R. acetosella* has long colpi. According to our own observations this morphological character is reasonably constant. However, short colpi occur not only in *R. acetosa*, but also in *R. alpestris*. Most other species have long colpi. Nevertheless this character is of great significance for the identification of a limited number of species.

(III) Endoaperture

In 3-colporate pollen there are normally 3 endopori. However, in pollen with a larger number of ectocolpi, often one or more endopores are missing under the centre of the ectocolpus. In fact, pollen with more than 4 ectocolpi usually have no more than 3 or 4 endopori.

The outline of the endoporus is also characteristic for many *Rumex* species. It is either circular (to slightly lalongate) or lolongate. This character is, however, only well observed if the colpus is exactly on top of the grain in equatorial view. In an oblique position it is often difficult to decide if an endoporus is circular or lolongate. Moreover, the character

is rather variable. In *R. crispus* some specimens have circular endopori, whereas in others the endopori are lologate.

(IV) *Costae endopori*

Costae endopori are present in the pollen of all species, but in some they are interrupted, breaking the circle around the endoporus into two halves (e.g. *R. acetosa*, *R. acetosella*). Complete costae are often present in grains with lologate endopori (*R. obtusifolius*, etc.).

(V) *Costae endocolpi*

All the species have pollen with very narrow, rather indistinct costae ectocolpi which usually run from the equator near to the end of the colpus. The significance from the identification point of view is, however, low because the feature is variable and difficult to observe.

(VI) *Size*

As usual, size is an unreliable feature in *Rumex* pollen. The variation in one sample may be relatively low, but variation between different samples of one species is often high. For this reason there is considerable overlap between the sizes of pollen of different species. On the other hand, because of the standard method used, it is possible to compare sizes to a certain extent. If there is an extreme difference it seems reasonable to use this to separate groups. Otherwise, size is a highly unreliable feature. Small sized pollen of *R. acetosa* and *R. acetosella* and related taxa can be separated from the large sized pollen such as *R. crispus*, *R. palustris*, etc. Pollen with aberrant sizes may occur in any species. Den Nijs et al. (1980) collected data of size differences of the pollen of *R. acetosella* specimens of the cytotypes $2N=14$, $2N=28$ and $2N=42$. He found that in higher ploidy levels the increase in diameter is unmistakable, but also that the overlap is considerable. We fully confirm his results (Table II).

(VII) *Reticulum*

Moore and Webb (1978) distinguish *R. acetosella* by the dupli- or pluricolumellate, slightly winding muri. These characters of the muri are not very consistent. In cytotypes with low chromosome numbers ($2N=14$ and $2N=28$) the muri are, indeed, more or less winding, al-

though in most specimens not duplicolumellate. On the other hand, in pollen of the cytotype $2N=42$ the muri are certainly not winding and clearly simplicolumellate. Their observations of columellae within the lumina could not be confirmed either in LM or in SEM. The lumina appear to be empty.

According to our observations the features of the reticulum are remarkably similar in the pollen of all *Rumex* species and could not, therefore, be used for the identification of species or groups.

(VIII) *Intruding colpi*

An interesting feature which is rather difficult to use, but probably fairly consistent, is the intruded position of the ectocolpi as seen in polar view. In fact, this character is often connected with the length of the colpi (either short or long) and is a useful additional character for the identification of *R. acetosa*, *R. acetosella* and *R. alpestris* pollen. In *R. crispus* this feature is of less use, as some specimens show pollen with intruding ectocolpi, whereas in other specimens the colpi do not intrude.

Andersen (1961) having studied the pollen of 18 European *Rumex* species recognized 4 pollen types:

(1) Pollen grains with short colpi (large polar area) were referred to the *R. acetosa* type in which he included *R. alpestris*.

In the present paper the *R. acetosa* group is comparable with the *R. acetosa* type of Andersen. We differ in including *R. thyrsiflorus* but excluding *R. alpestris*.

(2) Andersen includes *R. thyrsiflorus* in his *R. acetosella* type, but this species has long, distinctly intruding colpi and is better placed in the *R. acetosa* group.

(3) Andersen's third type is the *R. domesticus* type which includes *R. alpinus* (not studied here), *R. crispus*, *R. maritimus* and *R. obtusifolius*. *R. domesticus* is taken considered to be a synonym of *R. longifolius* and with *R. obtusifolius*, and *R. crispus* (p.p.) its pollen is arranged in the *R. obtusifolius* group. According to our observations *R. maritimus* belongs to another pollen group with 3-colporate pollen but, except for the difference in the number of

ectocolpi, its pollen resembles the *R. obtusifolius* group very closely.

(4) The fourth pollen type, the *R. aquaticus-hydrolapathum* type, differs from the *R. domesticus* type in its larger size and smaller pores. This pollen type is also recognized in this paper as a special group, the *R. aquaticus* group. On the whole, the ideas of Andersen are more or less confirmed by our study and have merely been developed further in this paper.

Birks (1973) also examined the pollen of 15 European *Rumex* species to which he added *Oxyria digyna*. He listed his results in a table without describing groups or types, which makes his table difficult to apply in pollen identification. In the text one type is mentioned, the *R. crispus* type which includes *R. longifolius*, *R. crispus*, *R. obtusifolius*, *R. conglomeratus* (p.p. psilate pollen with perforate tectum), *R. rupestris*, and *R. maritimus* (p.p. psilate pollen with perforate tectum). *R. pulcher* and *R. conglomeratus* are excluded. Some of his data are, however, in agreement with the information presented here. The large sized grains of *R. aquaticus* and *R. hydrolapathum* and the small ones of *R. acetosa* and *R. acetosella* (*R. alpestris*, and *R. thyrsoflorus* were not studied) are readily recognizable. Most other important data are highly abbreviated in codes based on the terminology of Iversen and Troels-Smith (1950). It is not easy to decipher these codes quickly, but one of them, P_{ac}, refers to the lolongate nature of the endoaperture. It is interesting that Birks also noticed a mixture of circular and lolongate endopori in *R. crispus*, an observation confirmed here. However, he also described some other species, such as *R. conglomeratus*, and *R. palustris* as having these two variations and we did not find them in these species. This confirms that the outline of the endoaperture is a character that has to be used with care.

After close examination of the pollen of 19 Northwest European *Rumex* species we found it possible to identify a number of pollen groups and individual species.

R. acetosa and *R. acetosella*, two species important for palaeoecological interpretation,

can be recognized by a combination of features; i.e. the colpus length, small size, features of the endopori and colpi intruding in equatorial view. *R. acetosa* is mainly recognized by its short colpi which do not intrude. *R. alpestris*, a species from montane zones, has pollen which resembles that of *R. acetosa*, but it differs in having a lolongate endoporus. On the other hand, pollen of *R. thyrsoflorus* a species from dry, open habitats in the lowland, resembles that of *R. acetosa* very much.

R. acetosella is characterized by its long, intruding colpi, small size and features of the endopori. Its cytotypes may differ in minor details, but can be recognized on the features mentioned above. *R. triangulivalvis* pollen is very close to this type, but differs in its slightly lolongate endopori.

Oxyria digyna pollen resembles that of *Rumex acetosella* very closely. It has distinctly intruding colpi, is small sized and has circular endopori. Nevertheless, there are differences and its pollen can be distinguished by the distinct, circular endopori, distinct columellae and muri of the reticulum and slightly larger size. Some of these features (larger size, distinct columellae) also occur in the cytotype $2N=42$, but those pollen grains are predominantly 4- or more-colporate, and the endopori are less distinct. According to Fredskild (1967) it is difficult to distinguish between *Rumex acetosella* and *Oxyria digyna* pollen in badly preserved material. Indeed, *Oxyria digyna* pollen most closely resembles that of *Rumex acetosella*, and both are readily distinguished from *R. conglomeratus* and *R. maritimus*, which were included in the *Oxyria* type of Faegri and Iversen (1974). 4-Colporate pollen can always be referred to *Rumex acetosella* as *Oxyria digyna* pollen is exclusively 3-colporate. The distinction between two 3-colporate forms is less easy, but they can best be identified by the columellae below the muri. In *Oxyria digyna* these are relatively coarse and distinct, whereas they are small and indistinct in *Rumex acetosella*. A second feature is the indistinct, usually interrupted and lolongate endoaperture of *Rumex acetosella* and the

circular, usually complete one of *Oxyria digyna*. In pollen found in sediments these endopori are, however, not always distinguishable.

Two closely related groups are the *R. sanguineus* group and the *R. conglomeratus* group. They are characterized by their size, a majority of 3-colporate pollen and distinct endopori, usually with closed costae. The groups are differentiated on the outline of the endopori. The *R. sanguineus* group has circular endopori, whereas the *R. conglomeratus* group has more or less lologate endopori. The two groups are also morphologically close to the *R. obtusifolius* group, which, however, has pantocolporate pollen. *R. crispus* pollen is aberrant in having specimens with either circular or lologate endopori. Moreover, the number of ectocolpi is highly variable. This has led us to classify its pollen under the *R. sanguineus* group as well as the *R. obtusifolius* group.

Following Andersen (1961), we have separated pollen of *R. aquaticus* and *P. hydrolapathum* into a special group. It is characterized by its large size, pantocolporate grains and coarse surface. These species often have abortive pollen which may well be linked to the high chromosome number ($2N = ca. 200$) in both species (Tutin, 1964).

The *R. obtusifolius* group is closely related to the *R. conglomeratus* group, differing only in its number of ectocolpi. For the same reason *R. palustris* pollen also has much in common with that of the *R. sanguineus* group.

Summarizing all the data, *Rumex* pollen is very uniform in overall shape (P/E ratio), apertural system and ornamentation (finely reticulate). It is possible to recognize groups of species and sometimes single species, but there is a good deal of overlap. The four groups of Andersen (1961) have been substantially confirmed; the additional groups and species we have identified are the result of taking a few refinements of the characters into account.

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Plate descriptions (all plates $\times 2000$, except where otherwise stated)

PLATE 1 (p.103)

Fagopyrum esculentum Moench (Arnolds 1681)

1. SEM micrograph; equatorial view.
2. SEM micrograph; ornamentation ($\times 10,000$).
3. Ornamentation in mesocolpium at high focus; reticulum.
4. Ornamentation in mesocolpium at medium focus; groups of infratectal columellae.
5. Ornamentation in mesocolpium at low focus; basal trunks.

PLATE 2 (p.104)

Fagopyrum esculentum Moench (figs.1–2, Arnolds 1681).

1. Equatorial view; cross-section, costae endocolpi, branched columellae.
2. Equatorial view; elongated, lalongate endocolpi with costae.

Fagopyrum tataricum (L.) Gaertner (figs.3–4, Lundberg s.n.).

3. SEM micrograph; equatorial view.
4. SEM micrograph; ornamentation ($\times 10,000$).

PLATE 3 (p.105)

Fagopyrum tataricum (L.) Gaertner (figs.1–6, Lundberg s.n.).

1. Equatorial view; cross-section, branched columellae.
2. Narrow, long colpus.
3. Polar view; cross-section, colpi not or only slightly sunken.
4. Endocolpus, lalongate with costae.
5. Ornamentation at high focus.
6. Ornamentation at low focus, indistinct basal trunks.

PLATE 4 (p.106)

Koenigia islandica L. (figs.1–2, Van der Knaap et al. 27a; figs.3–7, Oosterveld O.1108).

1. SEM micrograph; overall view with open pori.
2. SEM micrograph; overall view, pori closed.
3. Ornamentation at high focus.
4. Ornamentation at low focus, porus at high focus.
5. Porus at low focus.
6. Cross-section, rather large grain.
7. Cross-section, small grain.

PLATE 5 (p.107)

Polygonum amphibium L. (figs.1–2, Kertland s.n.; figs.3–5, Hekking s.n.).

1. SEM micrograph; overall view, colpi in regular pentagons.
2. SEM micrograph; colpus ($\times 5000$).
3. Ornamentation at high focus.
4. Ornamentation at medium focus; distinct granulae in lumina.
5. Ornamentation at low focus; columellae of ~~muting~~ two rows.

PLATE 6 (p.108)

Polygonum amphibium L. (fig.1, Hekking s.n.)

1. Cross-section.

Polygonum aviculare L. (figs.2, 6, Wilson 36; figs.3–5, Wilmott 534B)

2. SEM micrograph; cross-section of exine ($\times 5000$).
3. Polar view; cross-section at equator, sexine thicker than nexine in mesocolpium.
4. Ornamentation at high focus.
5. Ornamentation at low focus.
6. SEM micrograph; equatorial view.

PLATE 1 (*Fagopyrum esculentum* type: *F. esculentum*)

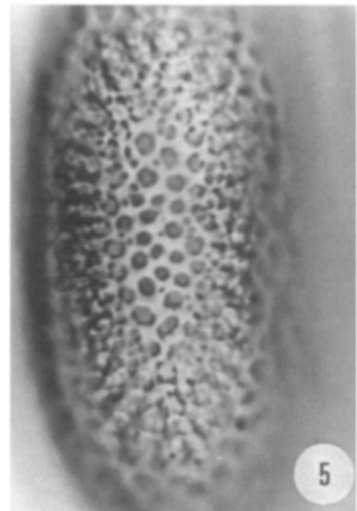
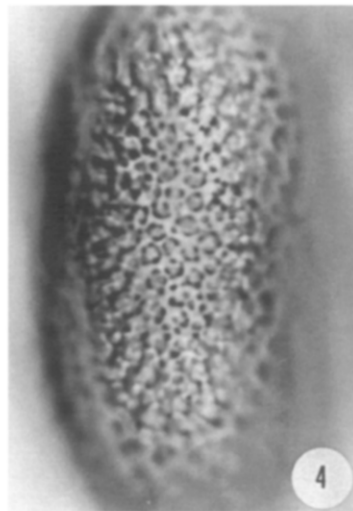
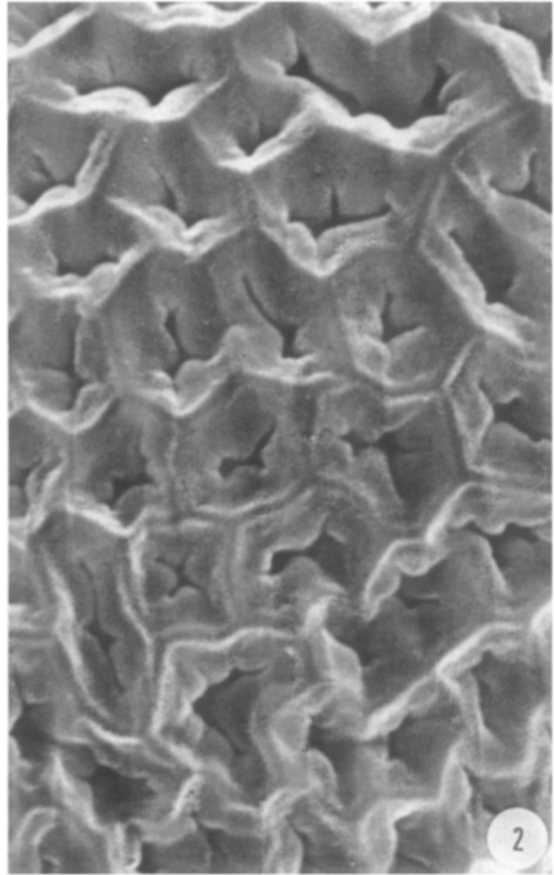
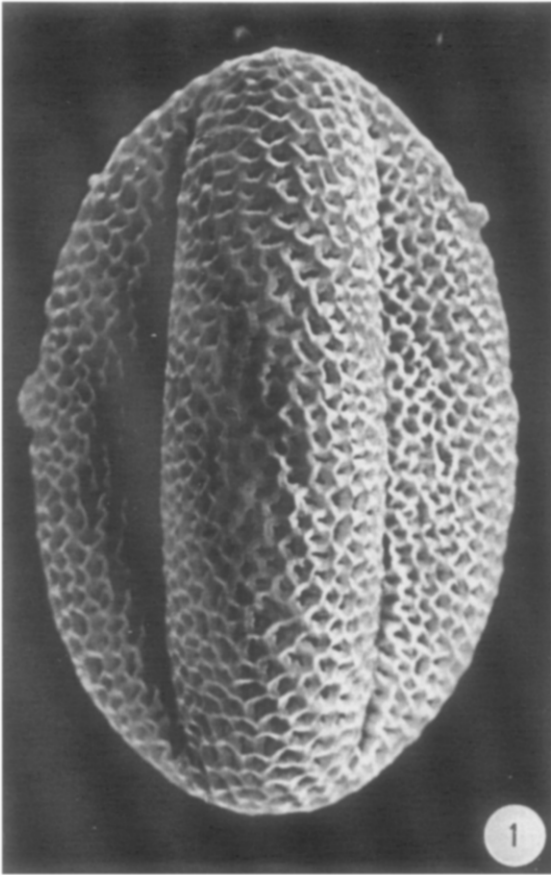


PLATE 2 (*Fagopyrum esculentum* type: *F. esculentum*. 1-2: *F. tataricum*. 3-4)

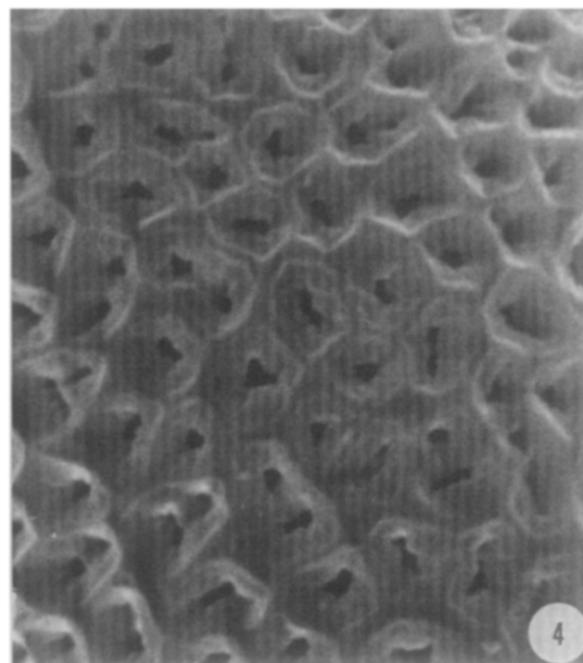
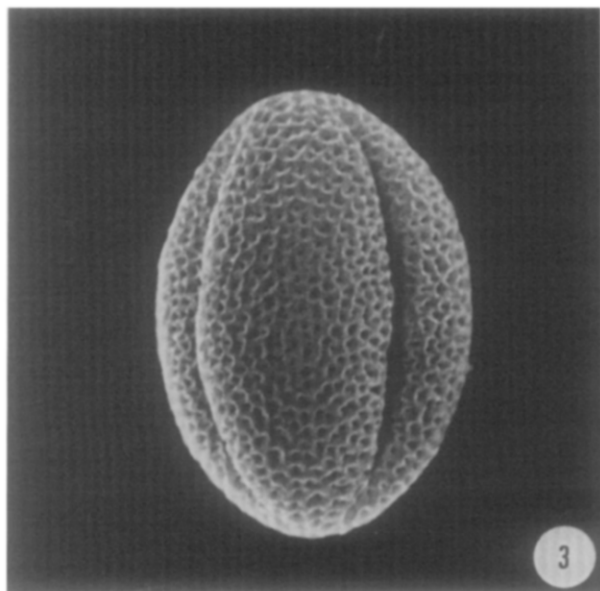
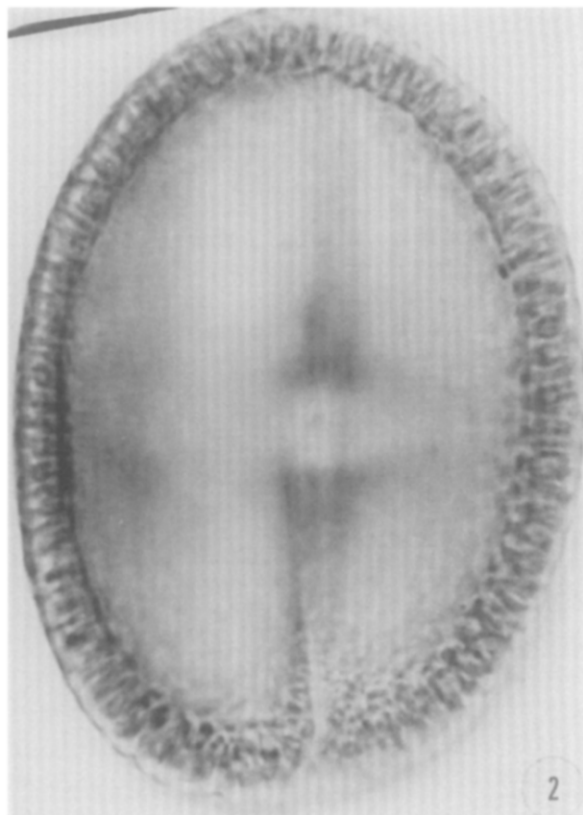
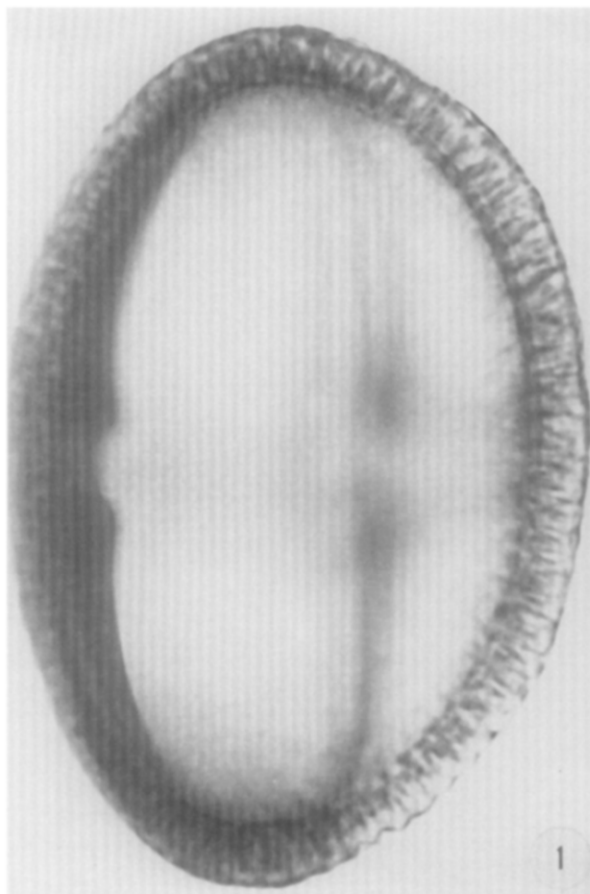


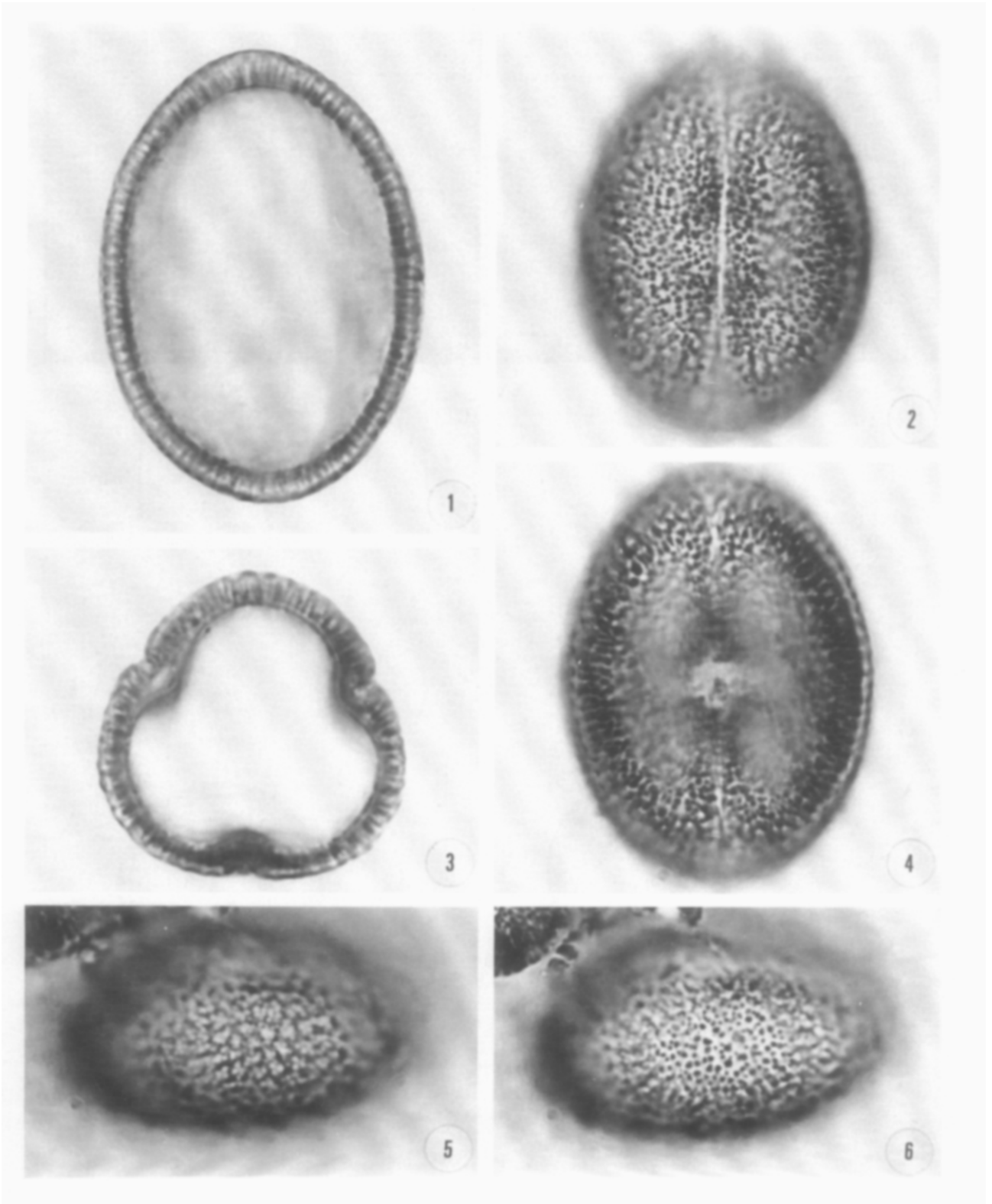
PLATE 3 (*Fagopyrum esculentum* type: *F. tataricum*)

PLATE 4 (*Koenigia islandica* type: *K. islandica*)

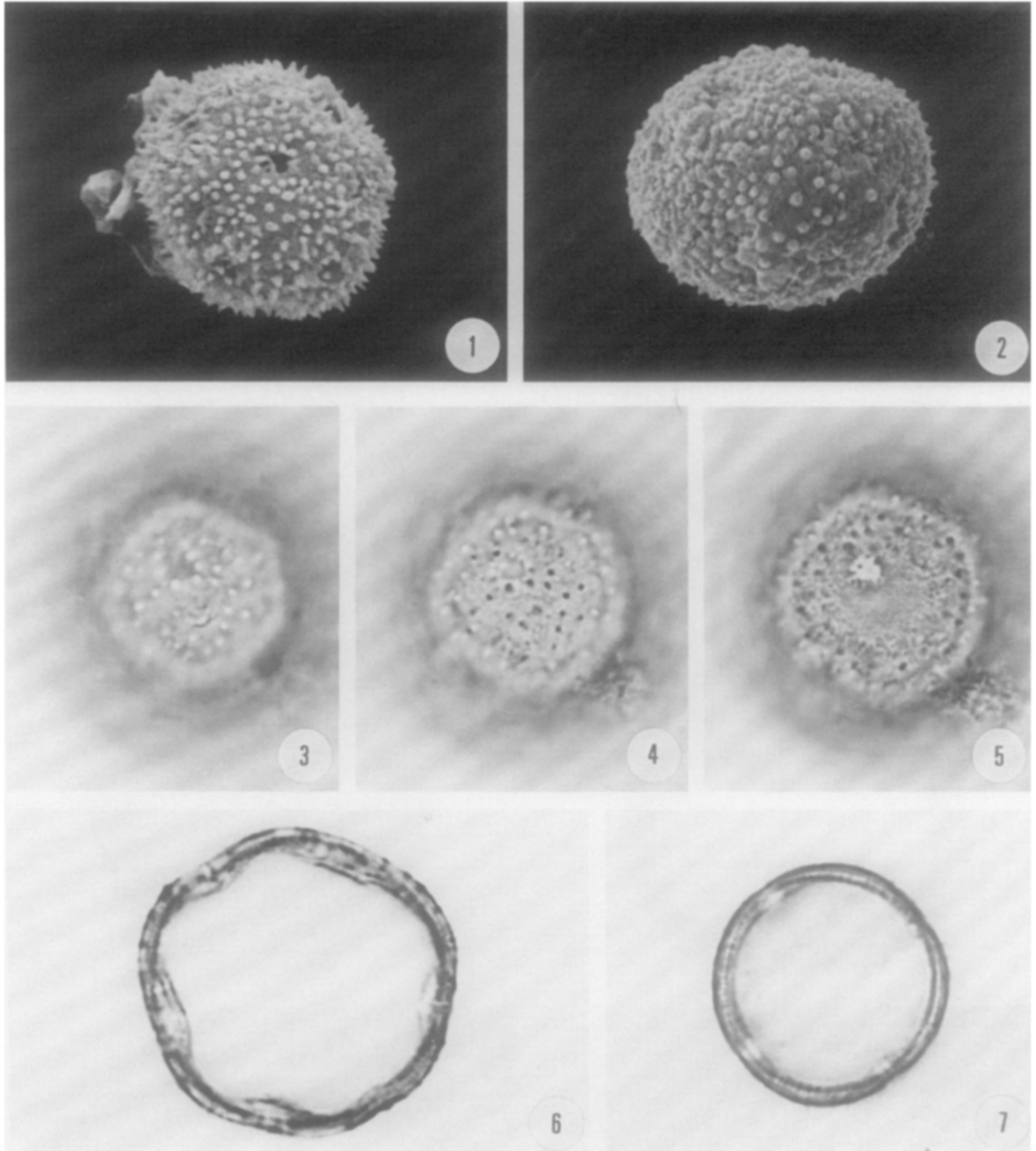


PLATE 5 (*Polygonum amphibium* type: *P. amphibium*)

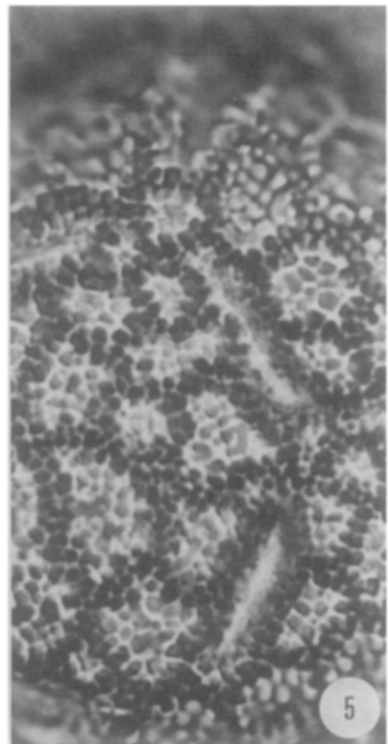
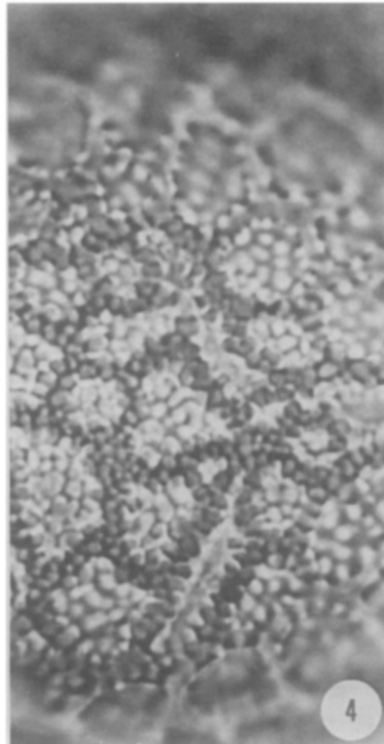
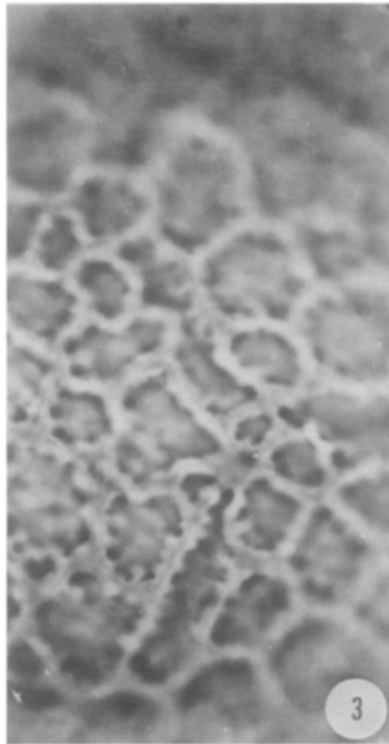
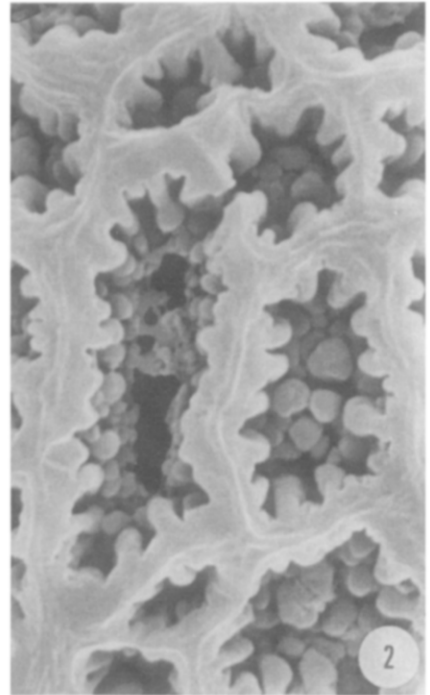
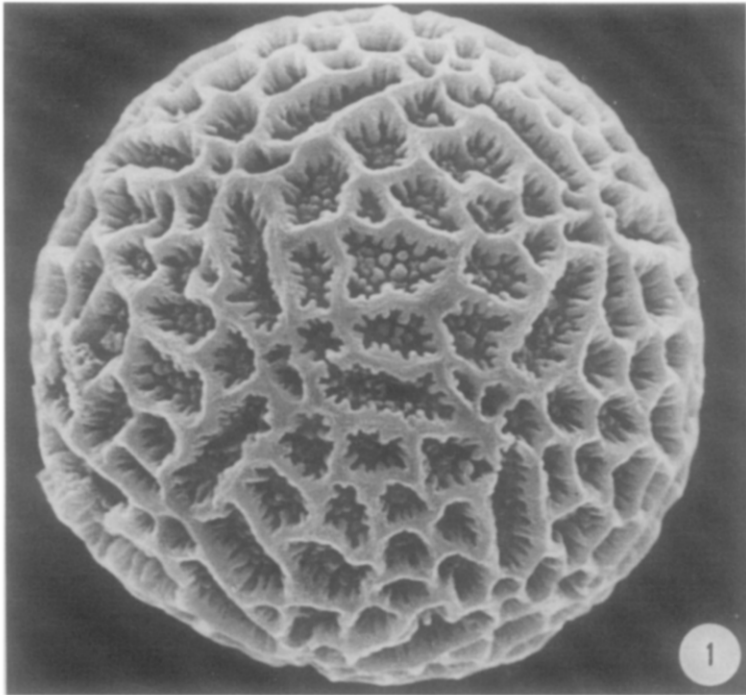


PLATE 6 (*Polygonum amphibium* type: *P. amphibium*, 1; *P. aviculare* type: *P. aviculare*, 2-6)

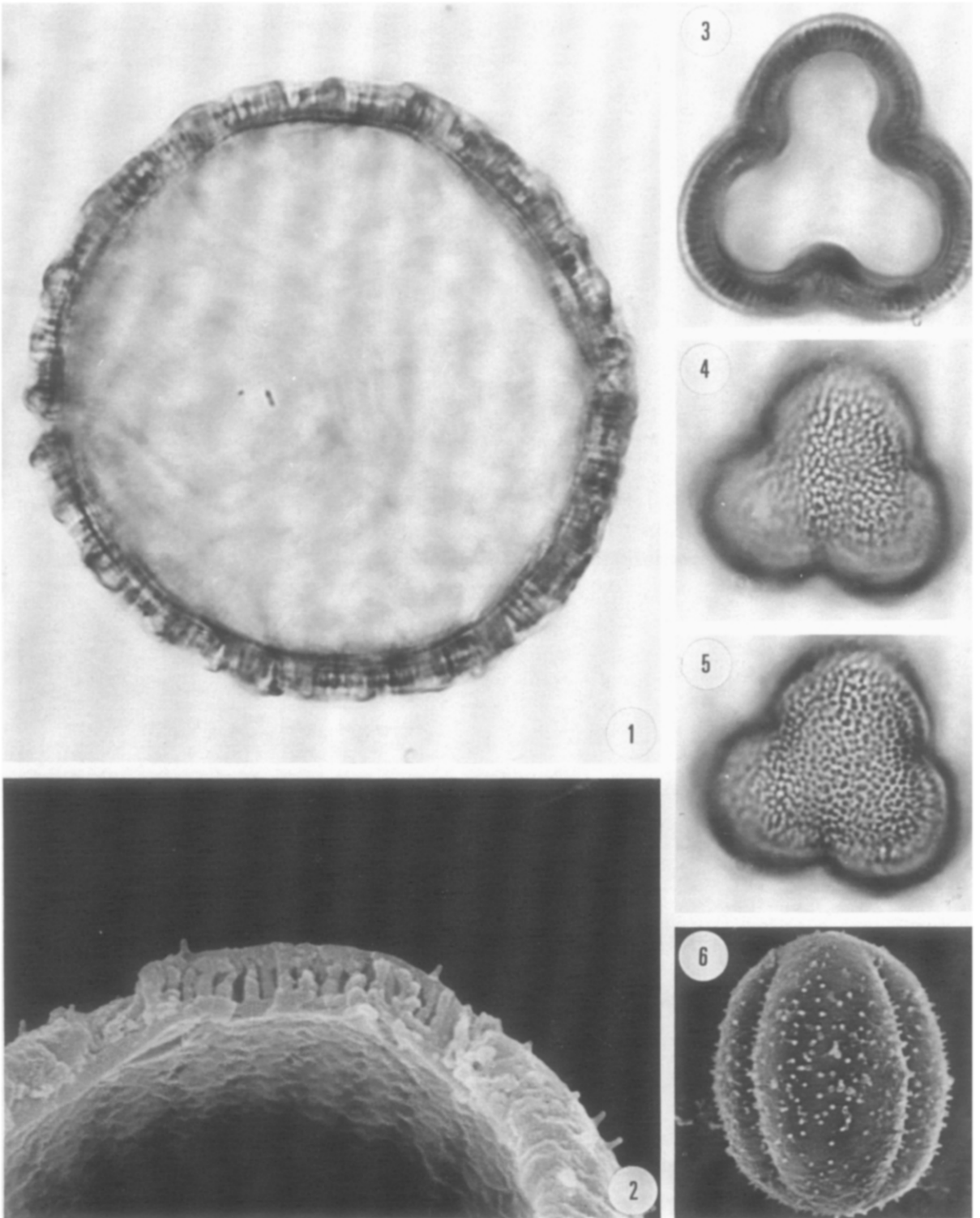


PLATE 7 (p.110)

Polygonum aviculare L. (figs.1–4, Wilmott 534B)

1. Colpus at high focus, margin of circular mesoaperture at high focus just visible.
2. Endocingulum.
3. Equatorial view; cross-section, distinct costae visible.
4. Mesoaperture.

Polygonum arenastrum Boreau (fig.5, Exc. Biol. Stud. 1964–635; figs.6–9, Exc. Biol. Stud. 1966–2623)

5. SEM micrograph; equatorial view.
6. Colpus at high focus.
7. Mesoaperture and endocingulum.
8. Equatorial view; cross-section with distinct costae.
9. Equatorial view; cross-section, sexine thicker than nexine, especially at poles.

PLATE 8 (p.111)

Polygonum boreale (Lange) Small (fig.1, Williams s.n.)

1. Equatorial view; cross-section, sexine thicker than nexine.

Polygonum maritimum L. (figs.2–4, Bento Rainha 3723; figs.5–7, Hunnybun 1427)

2. SEM micrograph; equatorial view, rather short colpus with endoaperture.
3. SEM micrograph; ornamentation ($\times 10,000$).
4. SEM micrograph; colpus with small granulae on colpus membrane.
5. Equatorial view; sexine thicker than nexine.
6. Colpus at low focus and tapering endocolpus, mesoaperture just visible.
7. Colpus at high focus.

PLATE 9 (p.112)

Polygonum oxyspermum Meyer et Bunge ex Ledebour ssp. *oxyspermum* (figs.1–2, 4, 6–9, Fries 668)

1. SEM micrograph; equatorial view of tricolporate grain.
2. SEM micrograph; pantocolporate grain.
4. SEM micrograph; ornamentation ($\times 10,000$).
6. Equatorial view; cross-section, sexine thicker than nexine.
7. Ornamentation; columellae at high focus.
8. Ornamentation; columellae at low focus.
9. Polar view; sexine distinctly thinner than nexine.

Polygonum oxyspermum Meyer et Bunge ex Ledebour ssp. *raii* (Babington) Webb et Chater (figs.3, 5, Alm 54)

3. Cross-section of pantocolporate grain.
5. Cross-section of tricolporate grain.

PLATE 10 (p.113)

Polygonum oxyspermum Meyer et Bunge ex Ledebour ssp. *raii* (Babington) Webb et Chater (figs.1, 2, Alm 54)

1. Colpus without endoaperture.
2. Colpus with endocolpus in loxo-position.

Polygonum patulum Bieberstein (fig.3, Sutter vL 425; figs.4–5, 7, Bakhuizen v.d. Brink 5390)

3. SEM micrograph; equatorial view.
4. Endocolpus and mesoaperture.
5. Endocolpus with horn.
7. Equatorial view.

Polygonum rurivagum Jordan ex Boreau (fig.6, 8, Hessel et al. 2206)

6. SEM micrograph; equatorial view.
8. SEM micrograph; ornamentation ($\times 10,000$).

PLATE 11 (p.114)

Polygonum rurivagum Jordan ex Boreau (figs.1–2, 5, Héribaud-Joseph s.n.)

1. Colpus at high focus.
2. Mesoaperture distinct, endocingulum vague.
5. Cross-section of pantocolporate grain, sexine thicker than nexine.

(continued on p.115)

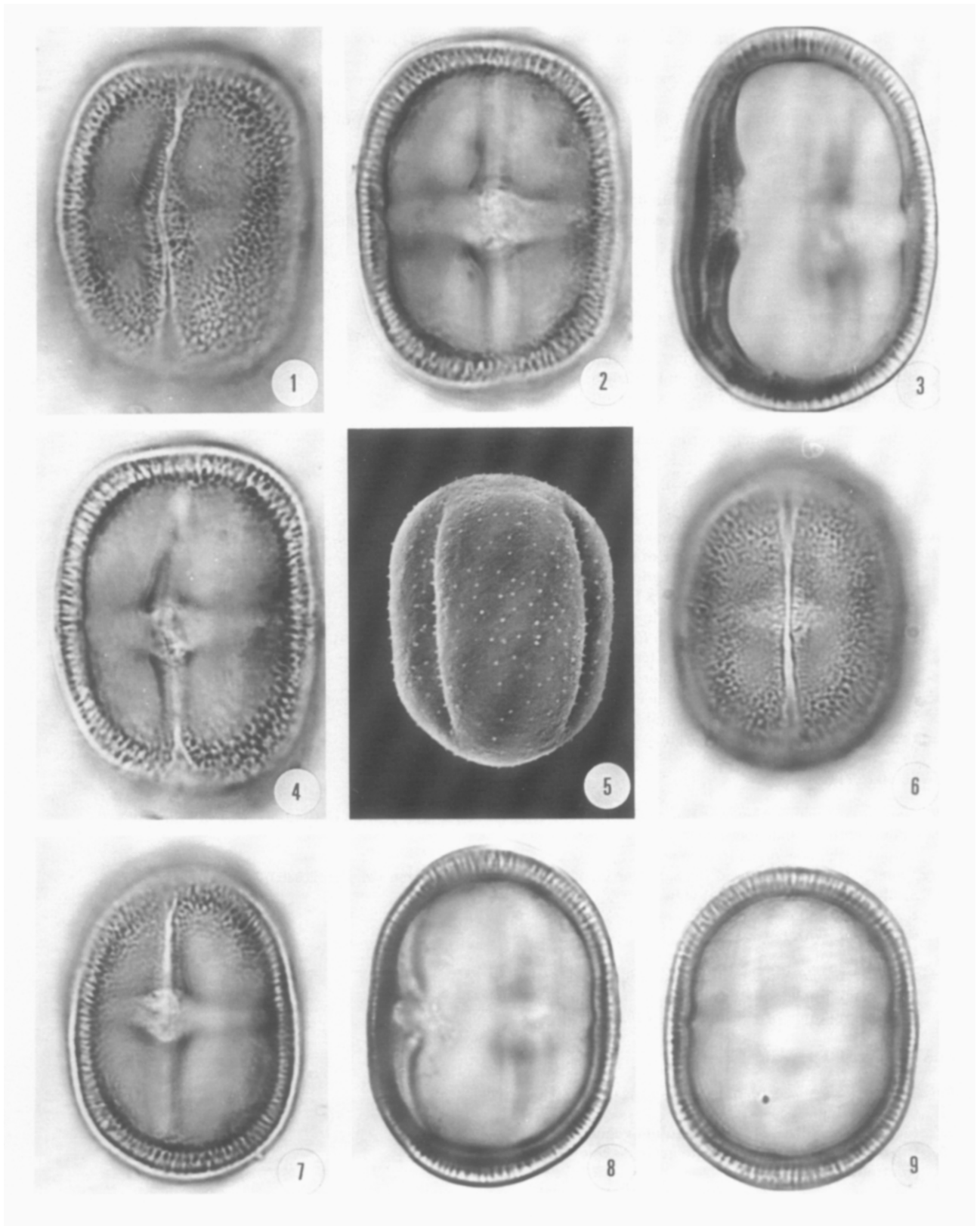
PLATE 7 (*Polygonum aviculare* type: *P. aviculare*, 1-4; *P. arenastrum*, 5-9)

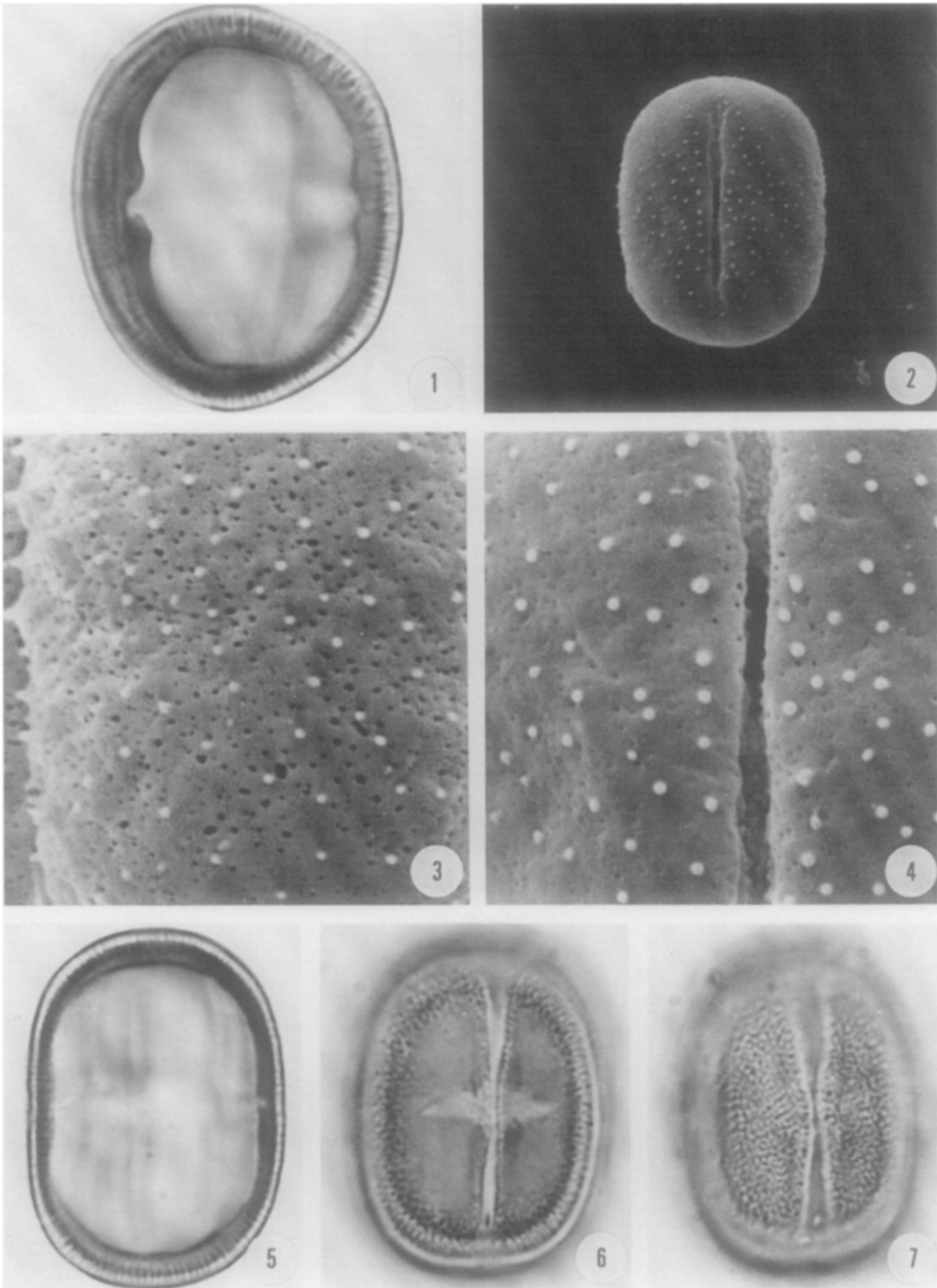
PLATE 8 (*Polygonum aviculare* type: *P. boreale*, 1; *P. maritimum*, 2-7)

PLATE 9 (*Polygonum aviculare* type: *P. oxyspermum* ssp. *oxyspermum*, 1-2, 4, 6-9; *P. oxyspermum* ssp. *raii*, 3,5)

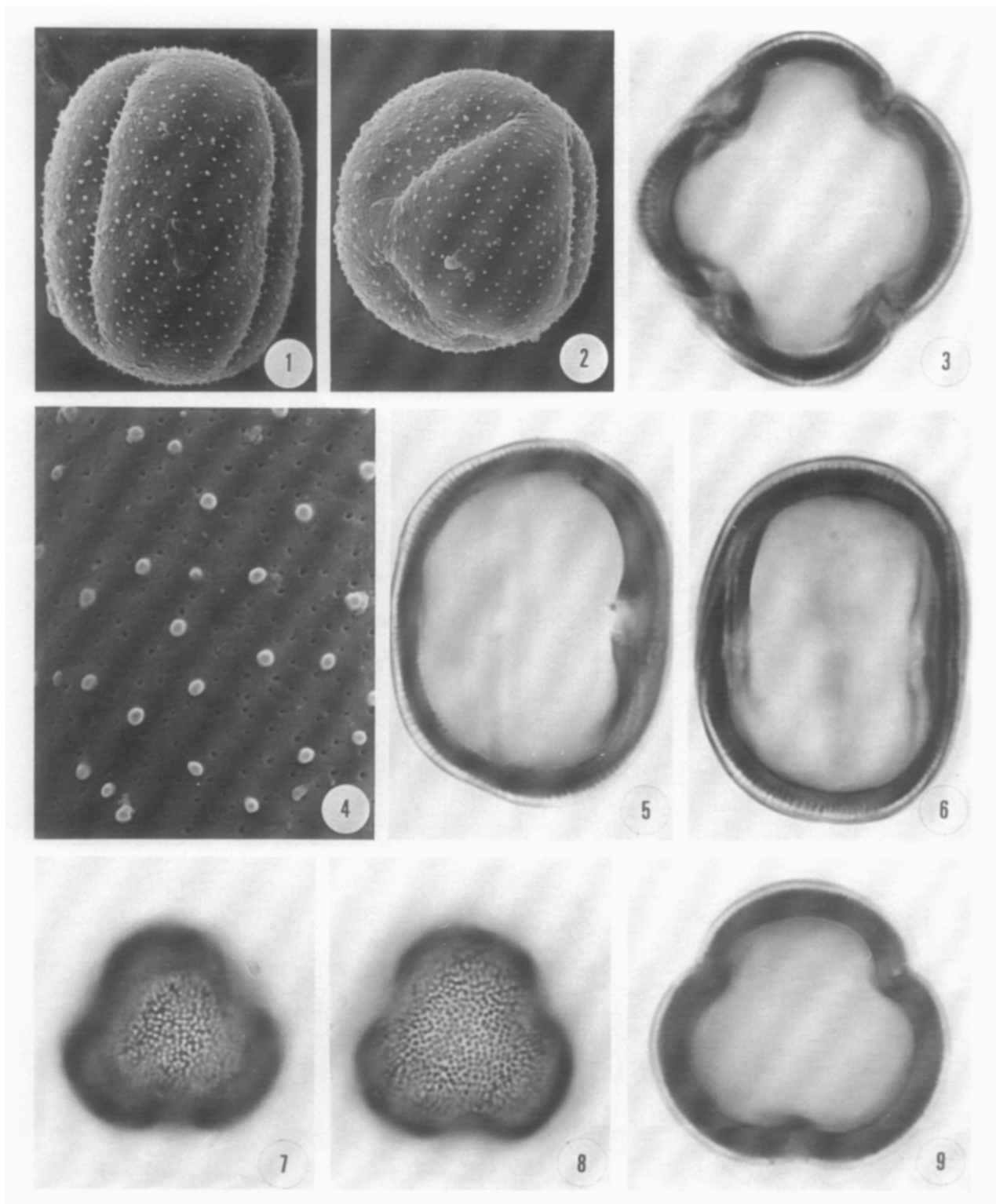


PLATE 10 (*Polygonum aviculare* type: *P. oxyspermum* ssp. *raii*, 1-2; *P. patulum*, 3-5, 7; *P. rurivagum*, 6, 8)

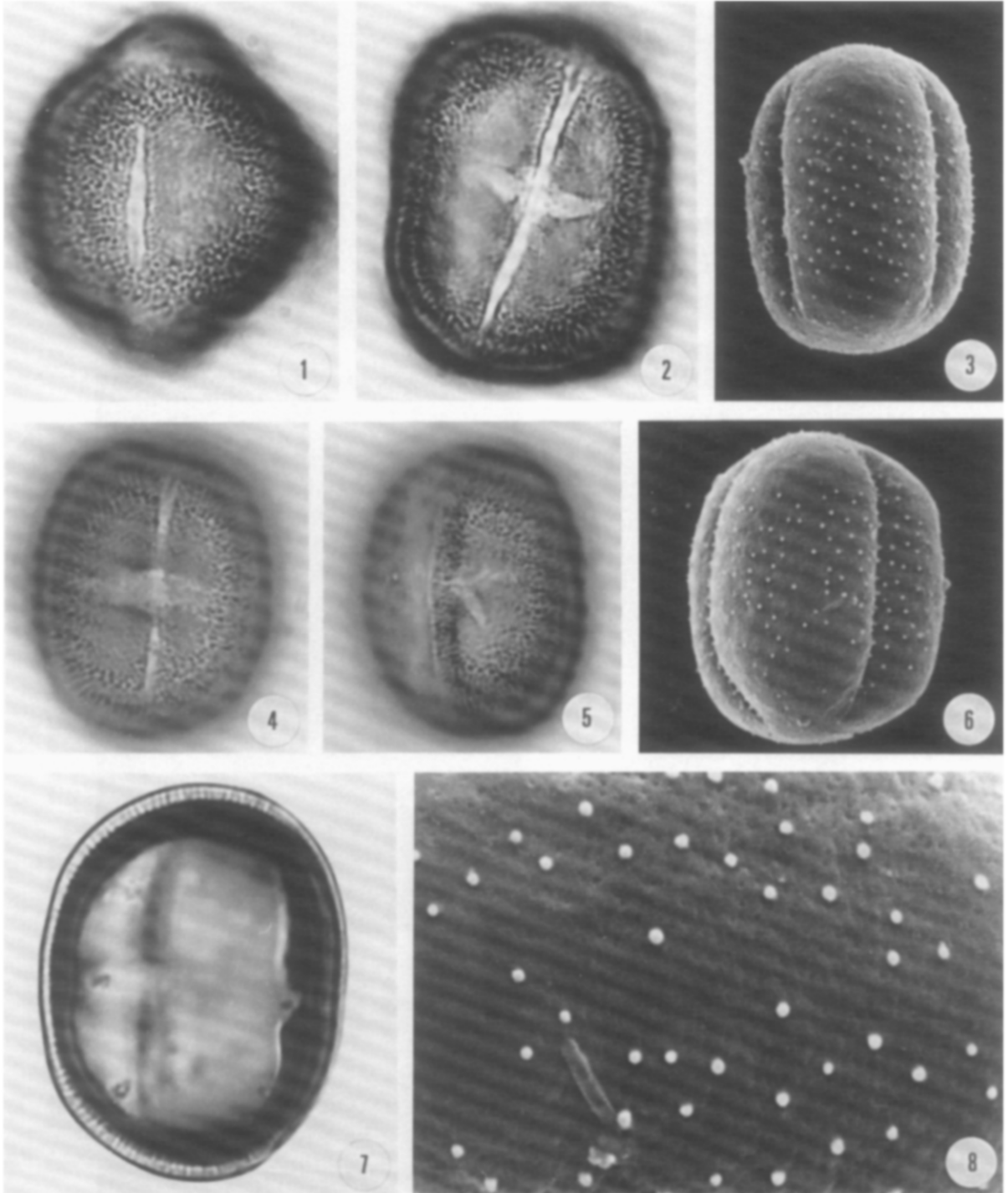
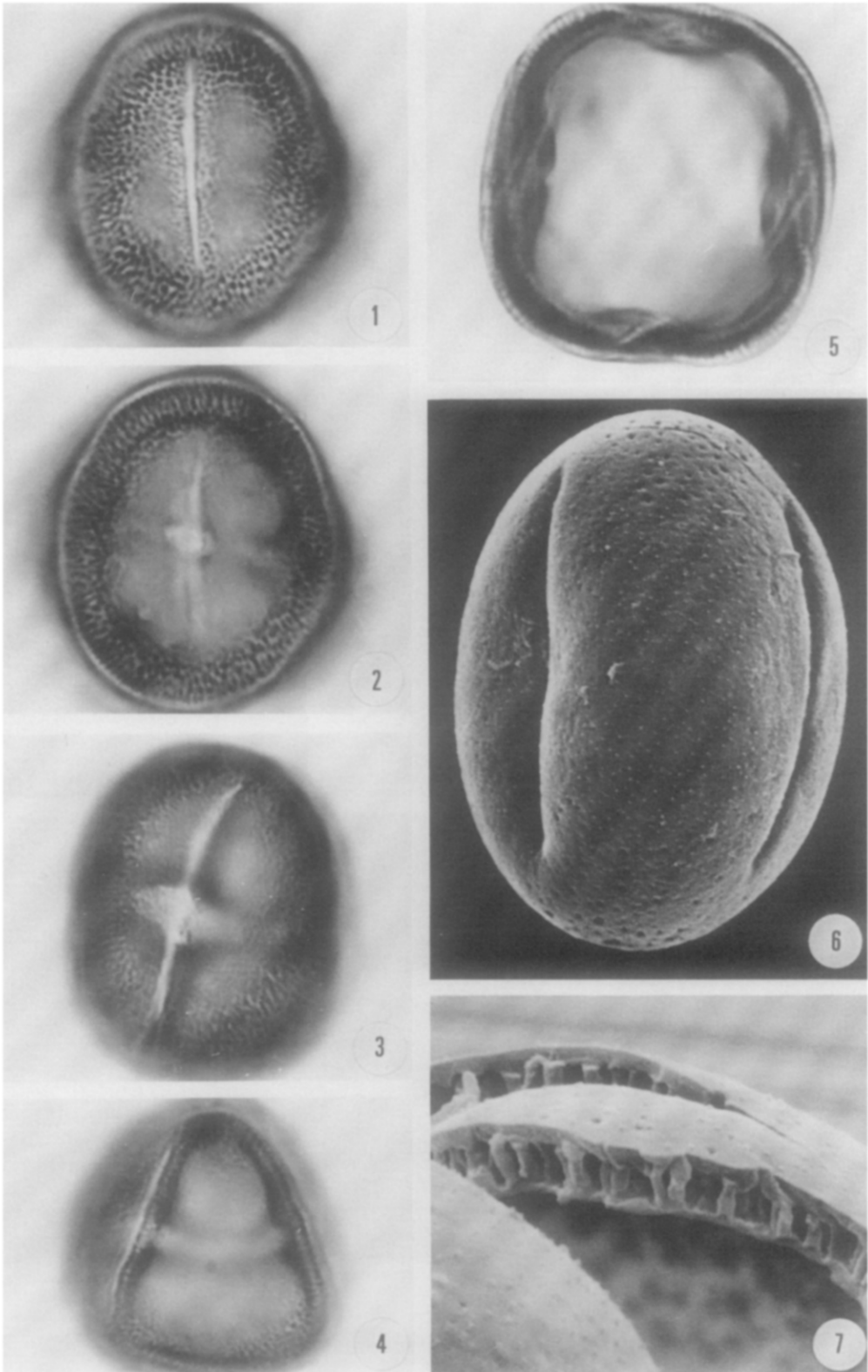


PLATE 11 (*Polygonum aviculare* type: *P. rurivagum*, 1, 2, 5; *P. oxyspermum* ssp. *raii*, 3-4; *Polygonum bistorta* type; *P. bistorta*, 6-7)



Polygonum oxyspermum Meyer et Bunge ex Ledebour ssp. *raii* (Babington) Webb et Chater (figs.3–4, Nannfeldt s.n.)

3. Colpus, mesoaperture and endocingulum.
4. Pantocolporate grain with distinct endocingulum.

Polygonum bistorta L. (figs.6–7, Exc. Biol. Stud. 1960–6)

6. SEM micrograph; equatorial view.
7. SEM micrograph; cross-section of exine ($\times 5000$)?.

PLATE 12 (p.116)

Polygonum bistorta L. (fig. 1, Ensink s.n.; figs.2–4 Exc. Biol. Stud. 1960–6)

1. Equatorial view; cross-section, branched columellae.
2. Colpus and endoaperture.
3. Polar view; ornamentation at high focus.
4. Polar view; ornamentation at low focus, channels between columellae broad and irregular.

PLATE 13 (p.117)

Polygonum viviparum L. (fig.1, 3–4, Oosterveld 0916; fig.2, Mennega s.n.)

1. SEM micrograph; equatorial view.
2. Equatorial view; cross-section, costae narrow but distinct.
3. Polar view; ornamentation at high focus.
4. Polar view; ornamentation at high focus, channels between columellae narrow.

PLATE 14 (p.118)

Polygonum viviparum L. (fig.1, Mennega s.n.; fig.2, Oosterveld 0916)

1. Colpus with elongated endoaperture, costae narrow but distinct, ends indistinct.
2. Equatorial view; cross-section, sexine thicker at poles than near equator.

Polygonum amplexicaule Don (figs.3–4, Renu Anand s.n.)

3. Colpus with elongated endoaperture, costae narrow but distinct, ends indistinguishable.
4. Equatorial view; cross-section, sexine at poles only slightly thicker than near equator.

PLATE 15 (p.119)

Polygonum amplexicaule Don (figs.1–3, Renu Anand s.n.)

1. Polar view; cross-section.
2. Polar view; ornamentation at high focus.
3. Polar view; ornamentation at low focus, channels between columellae narrow.

Polygonum convolvulus L. (figs.4, 6–7, Hessel et al. 1185; fig.5, Van Royen 360)

4. SEM micrograph; ornamentation around colpus (margo).
5. SEM micrograph; equatorial view with colpus and margo.
6. SEM micrograph; equatorial view of mesocolpium.
7. SEM micrograph; polar view.

PLATE 16 (p.120)

Polygonum convolvulus L. (figs.1, 7, Behrendsen s.n.; figs.2–3, Van Royen 360; figs.4–5 Gerrans 1294)

1. Equatorial view; endocingulum.
2. Colpus and endoaperture with distinct costae.
3. Equatorial view; cross-section, columellae at poles distinctly higher than at equator.
4. Polar view; ornamentation at high focus.
5. Polar view; ornamentation at low focus.
7. Polar view; cross-section, nexine thicker than sexine.

Polygonum dumetorum L. (figs.6, 9, Hume 1322; fig.8, Todaro 670)

6. Polar view; cross-section.
8. SEM micrograph; polar view.
9. Equatorial view; cross-section, columellae at poles distinctly higher than at equator.

PLATE 12 (*Polygonum bistorta* type: *P. bistorta*)

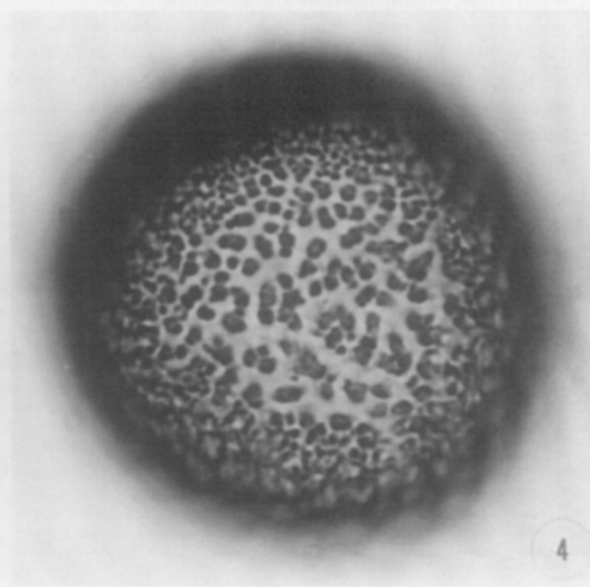
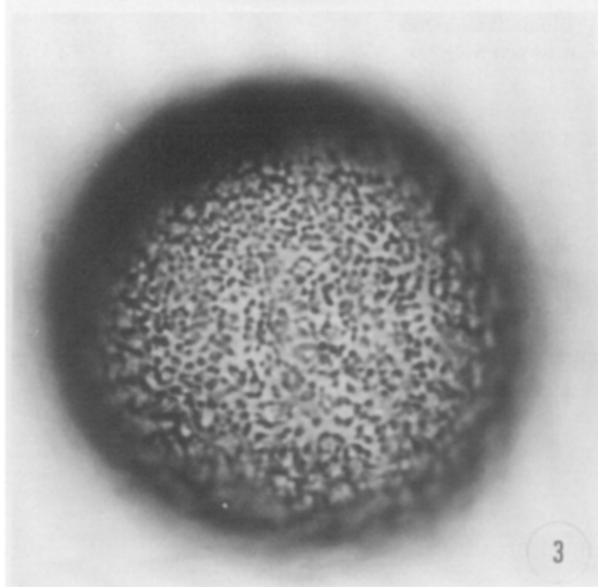
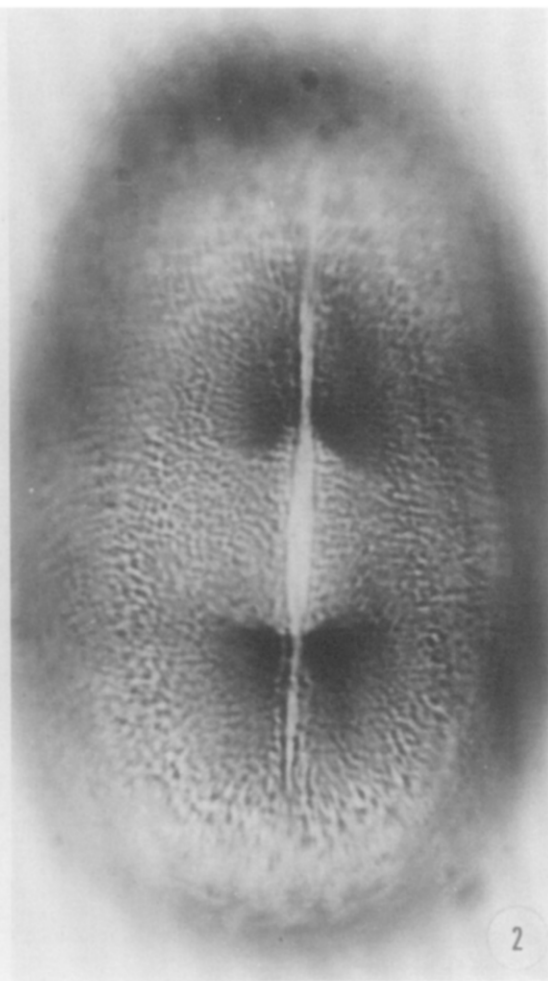


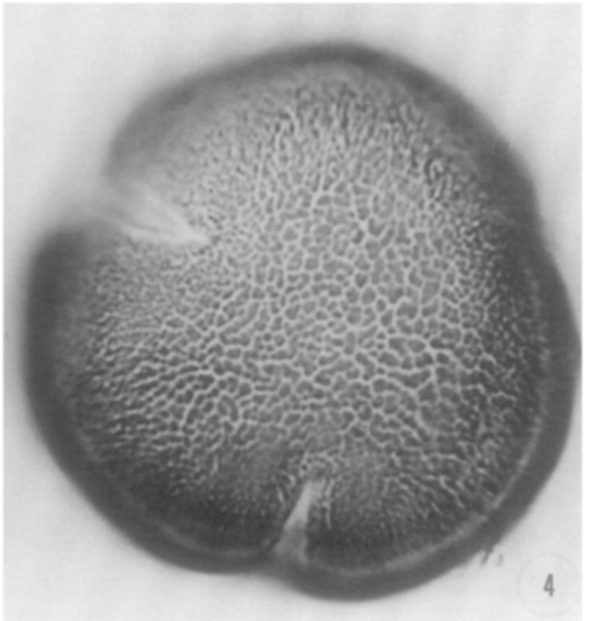
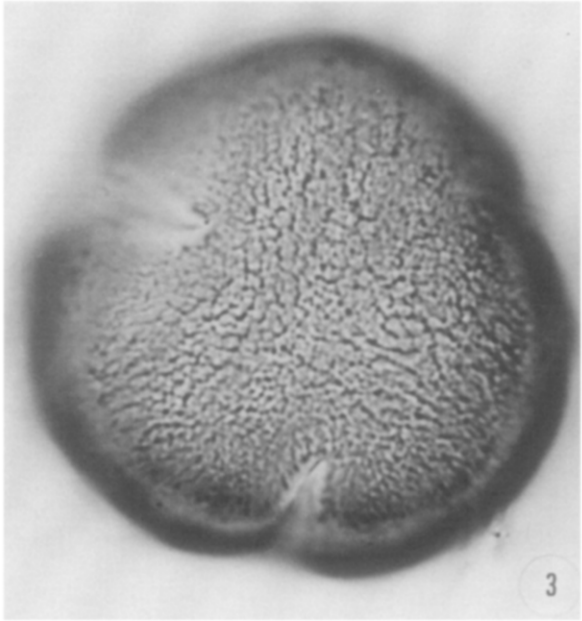
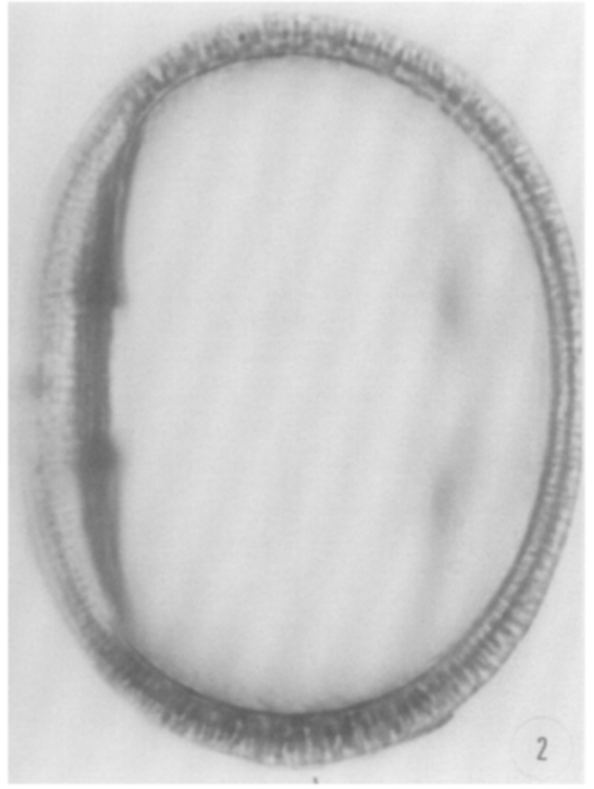
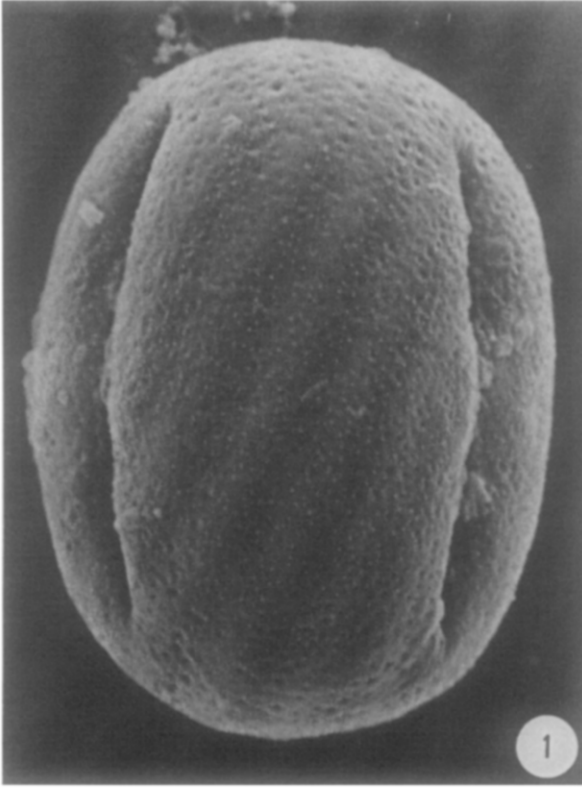
PLATE 13 (*Polygonum bistorta* type: *P. viviparum*)

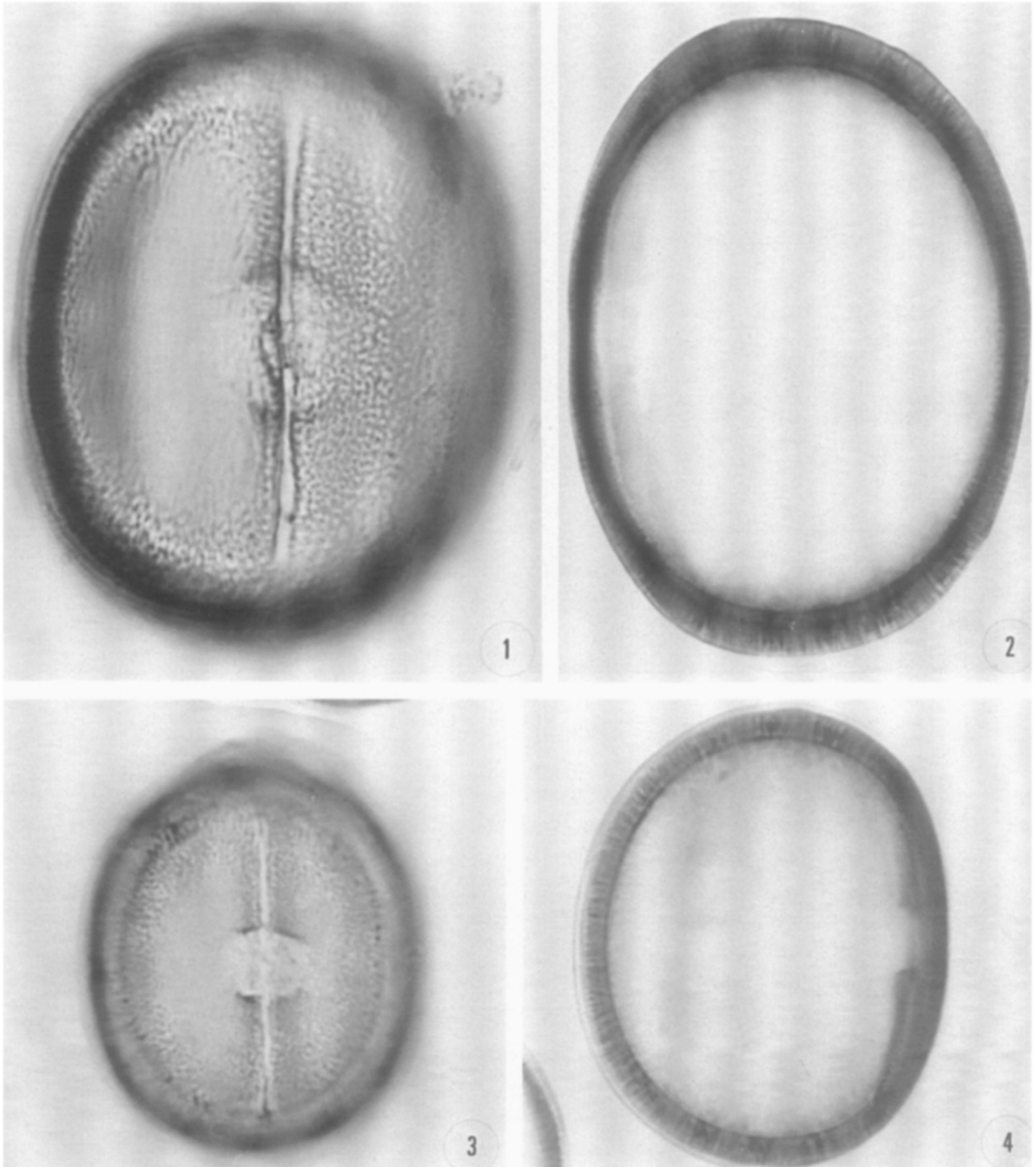
PLATE 14 (*Polygonum bistorta* type: *P. viviparum*, 1-2; *P. amplexicaule*, 3-4)

PLATE 15 (*Polygonum bistorta* type: *P. amplexicaule*, 1-3; *Polygonum convolvulus* type: *P. convolvulus*, 4-7)

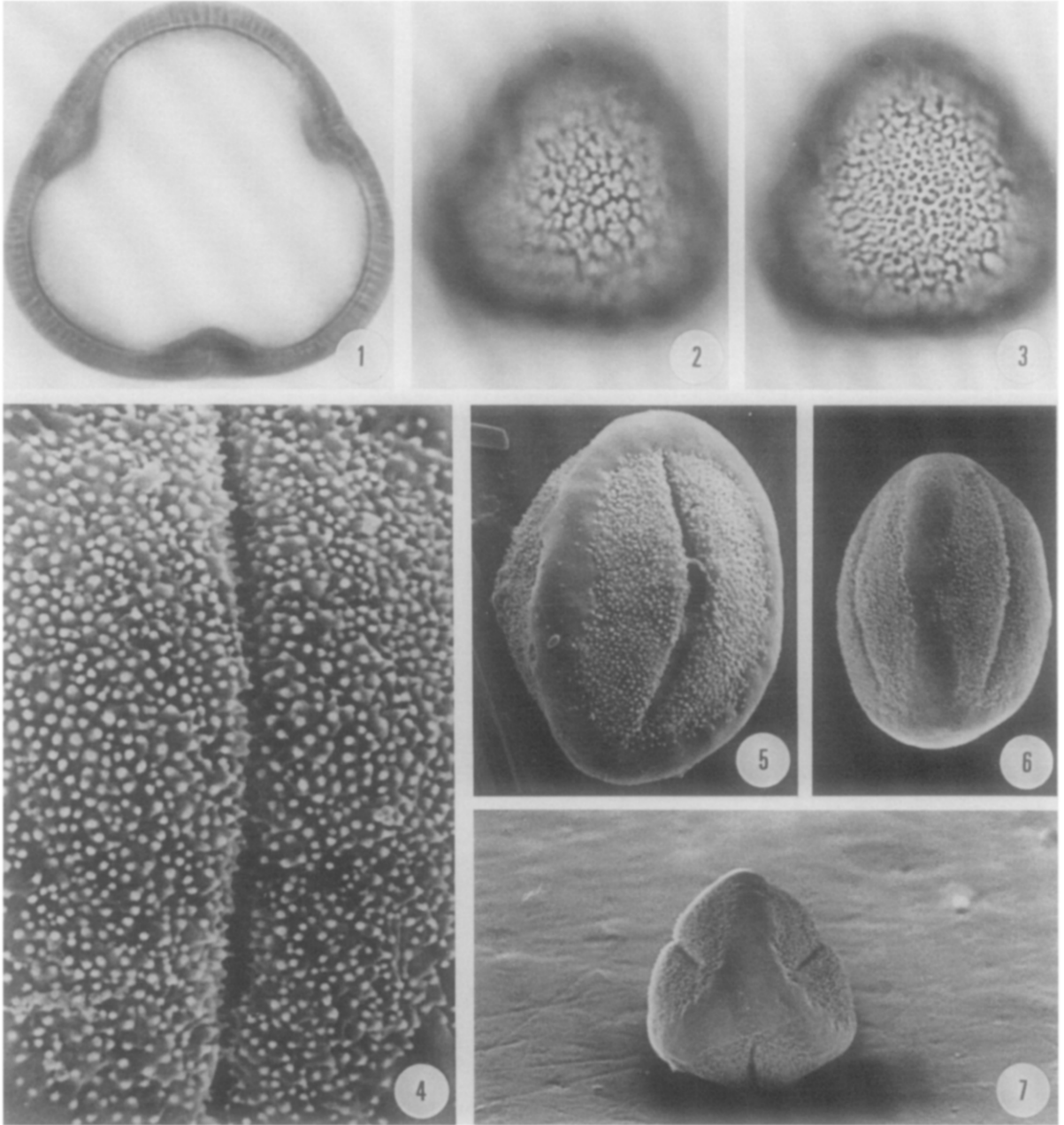


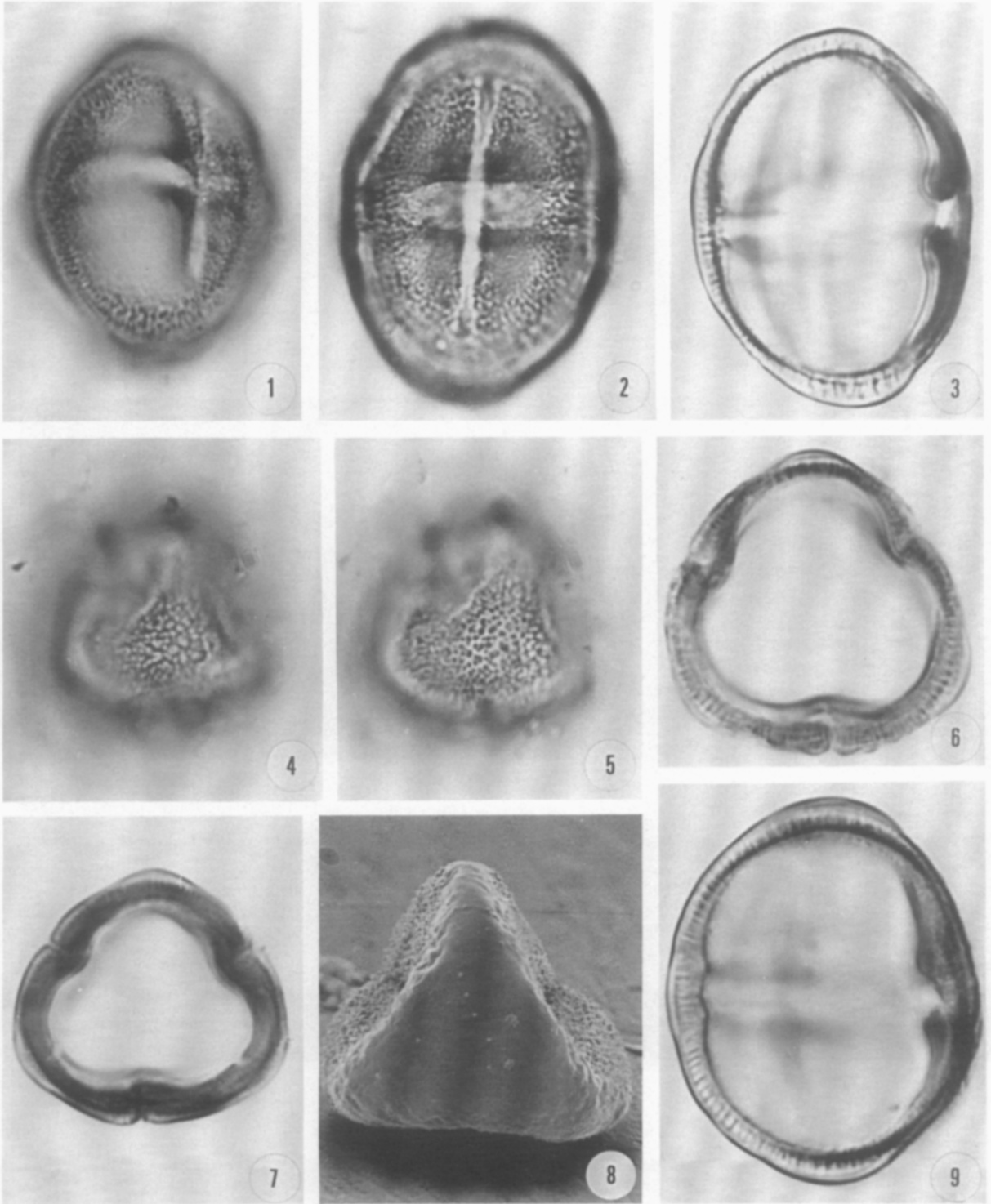
PLATE 16 (*Polygonum convolvulus* type: *P. convolvulus* 1-5, 7; *P. dumetorum*, 6, 8-9)

PLATE 17 (p.122)

Polygonum persicaria L. (figs.1–3, Miquel s.n.; figs.4–8, Swart 1846)

1. SEM micrograph; overall view.
2. SEM micrograph; porus and reticulum ($\times 10,000$).
3. SEM micrograph; cross-section of exine ($\times 10,000$).
4. Ornamentation at highest focus, muri at top.
5. Ornamentation at high focus, narrow muri.
6. Ornamentation at medium focus, columellae at high focus.
7. Ornamentation at low focus, columellae at medium focus, granules at top focus.
8. Ornamentation at lowest focus, columellae at low focus, granules at low focus.

PLATE 18 (p.123)

Polygonum persicaria L. (fig.1, Swart 1846)

1. Cross-section.

Polygonum foliosum Lindberg (figs.2–5, Svenonius 573)

2. Ornamentation at medium focus, columellae at high focus.
3. Ornamentation at low focus, columellae at low focus.
4. SEM micrograph; overall view.
5. SEM micrograph; porus in large lumen of reticulum ($\times 10,000$).

PLATE 19 (p.124)

Polygonum foliosum Lindberg (fig.1, Lindberg s.n.)

1. Cross-section; columellae rounded at their tops.

Polygonum hydropiper L. (fig. Hessel et al. 1655)

2. SEM micrograph; overall view.

PLATE 20 (p.125)

Polygonum lapathifolium L. (figs.1, 6, Hessel et al. 1773; figs.2–5 Hekking s.n.)

1. SEM micrograph; overall view.
2. Cross-section of ellipsoid grain.
3. Porus and ornamentation at high focus.
4. Porus and ornamentation at medium focus.
5. Porus and ornamentation at low focus.
6. SEM micrograph; porus and ornamentation ($\times 10,000$).

PLATE 21 (p.126)

Polygonum minus Hudson (fig.1, Hessel et al. I-32; fig.2, Koopmans 542; figs.3–6 Lejeune et Courtois 267)

1. SEM micrograph; overall view.
2. Cross-section.
3. Ornamentation, columellae at high focus.
4. Ornamentation, columellae at medium focus.
5. Ornamentation, columellae at low focus, granulae at high focus.
6. Ornamentation, columellae at lowest focus, granulae at low focus.

PLATE 22 (p.127)

Polygonum mite Schrank (fig.1, Wasscher s.n.; fig.2, Mennega s.n.)

1. SEM micrograph; overall view.
2. Cross-section.

PLATE 23 (p.128)

Polygonum mite Schrank (fig.1, Wasscher s.n.; figs.2–3, Mennega s.n.)

1. SEM micrograph; cross-section of exine ($\times 10,000$).
2. Ornamentation, columellae at medium focus, porus at high focus.
3. Ornamentation, columellae at low focus, porus at low focus.

PLATE 17 (*Polygonum persicaria* type: *P. persicaria*)

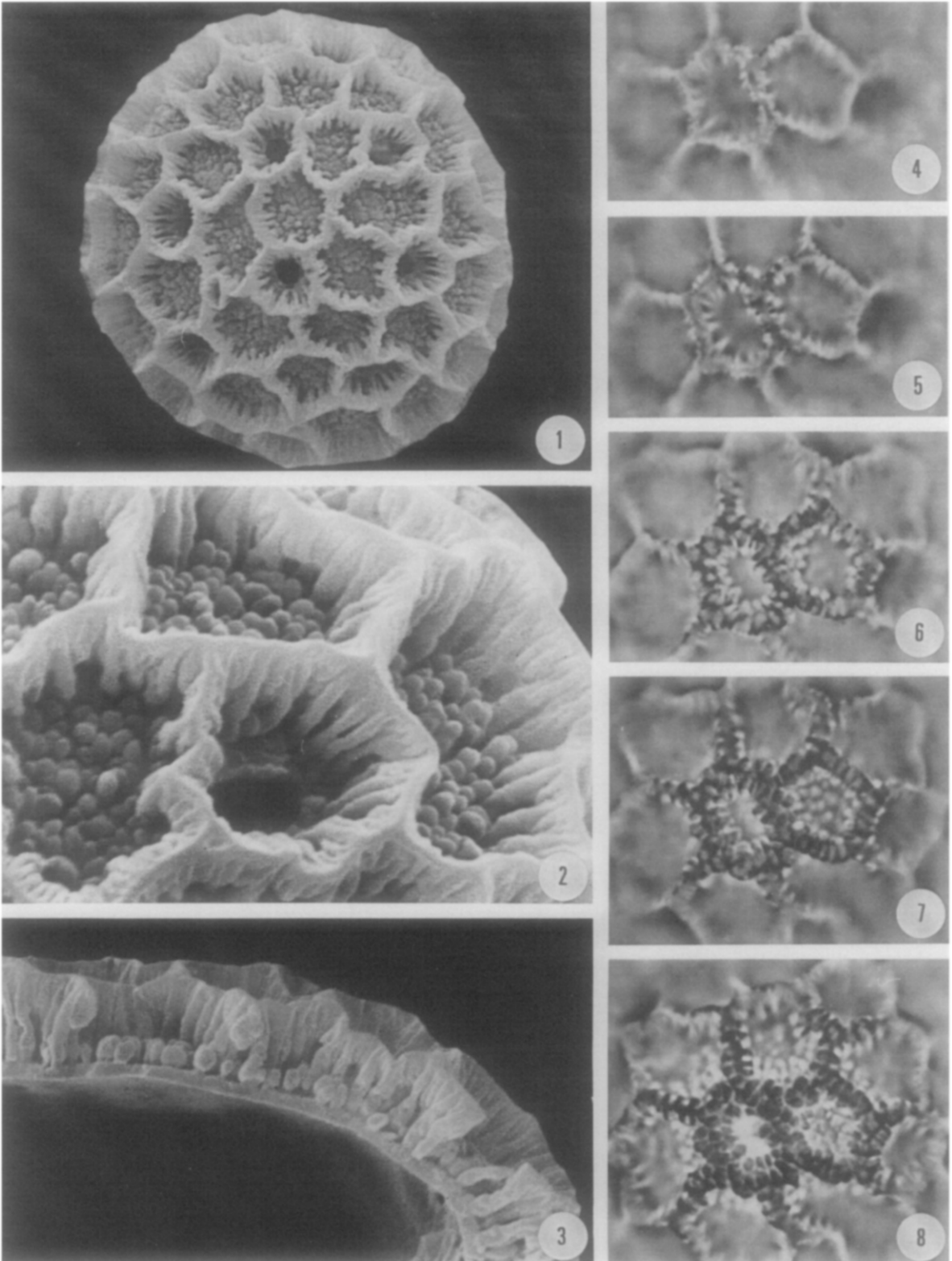


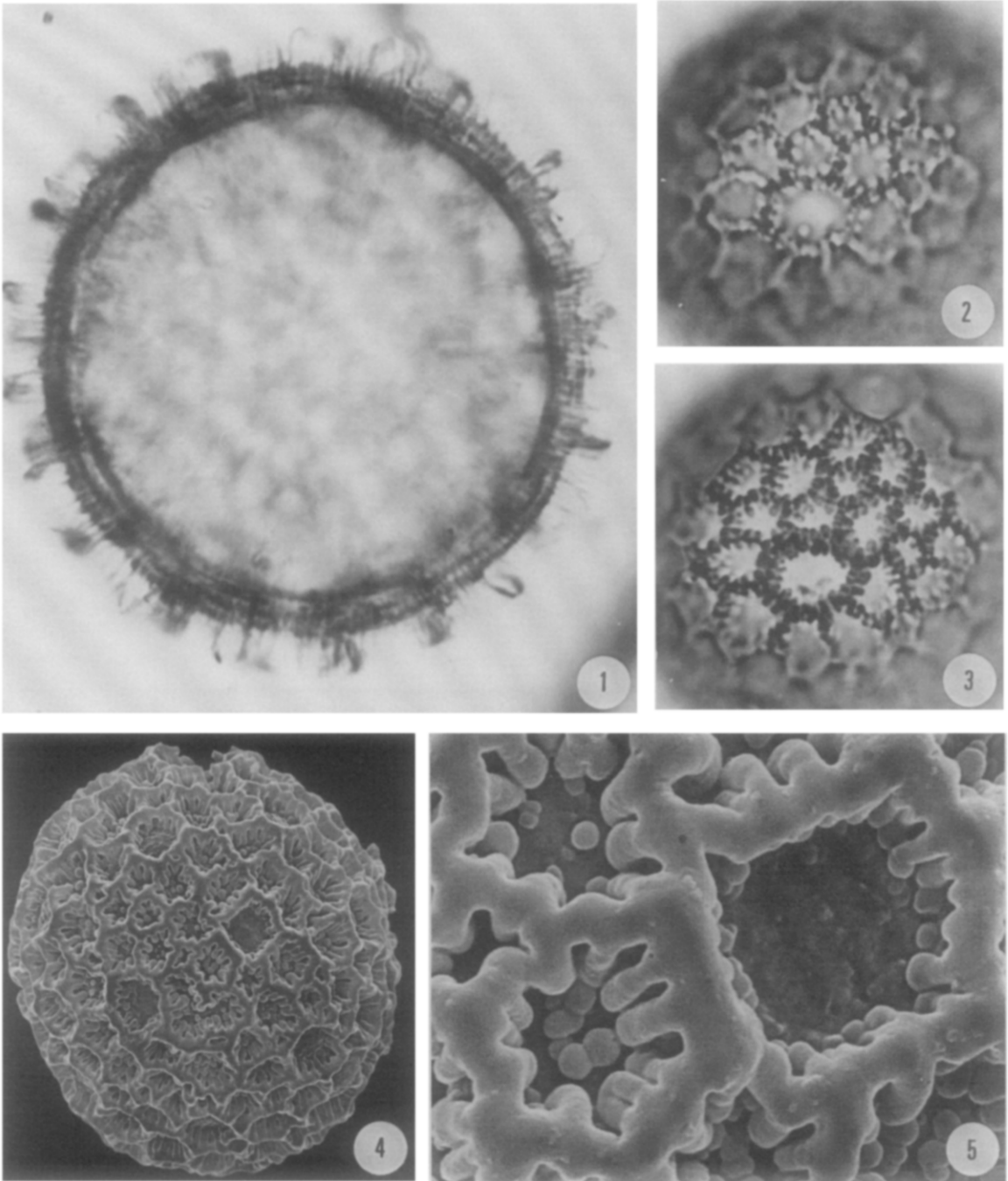
PLATE 18 (*Polygonum persicaria* type: *P. persicaria*, 1; *P. foliosum*, 2-5)

PLATE 19 (*Polygonum persicaria* type: *P. foliosum*, 1; *P. hydropiper*, 2)

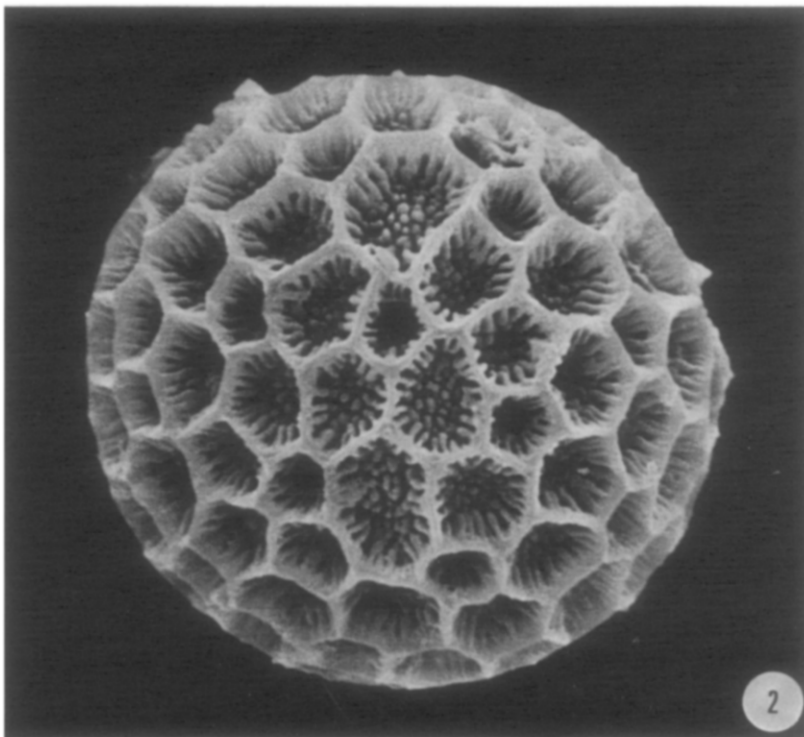
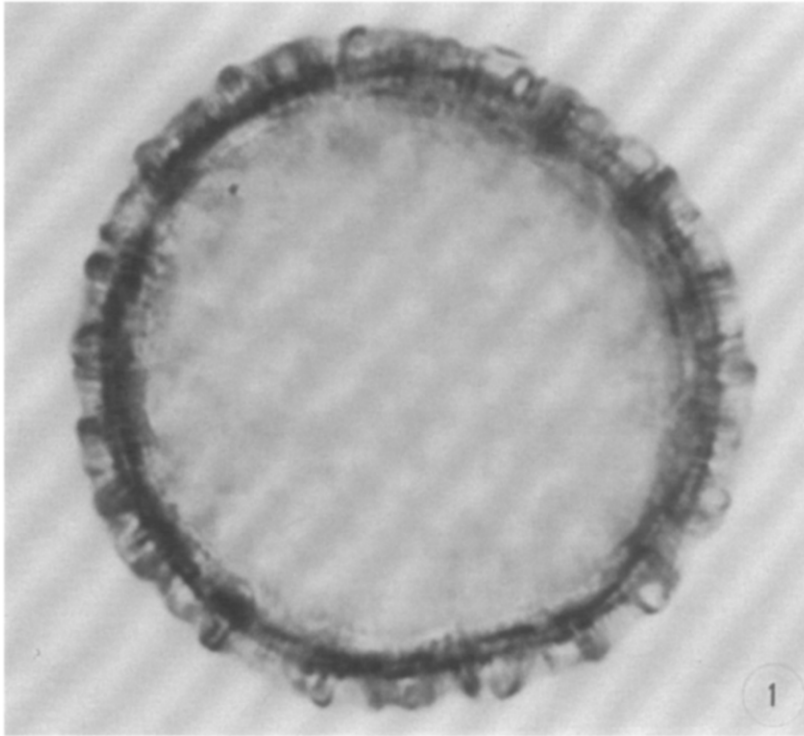


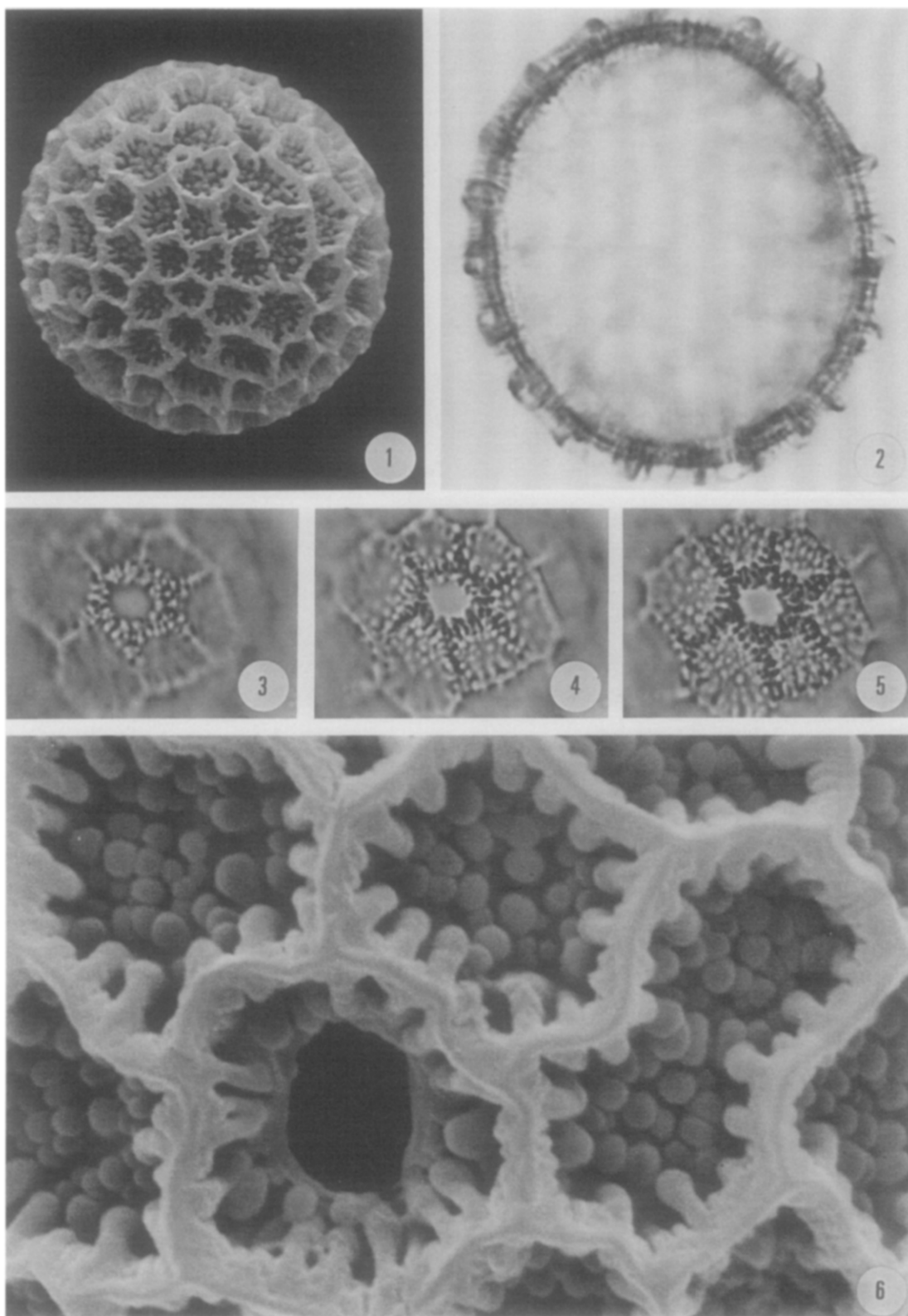
PLATE 20 (*Polygonum persicaria* type: *P. lapathifolium*)

PLATE 21 (*Polygonum persicaria* type: *P. minus*)

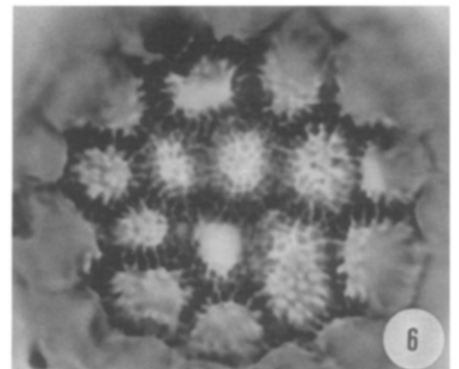
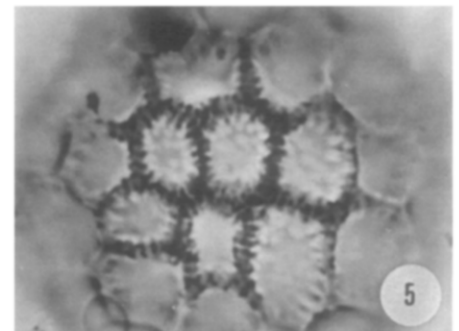
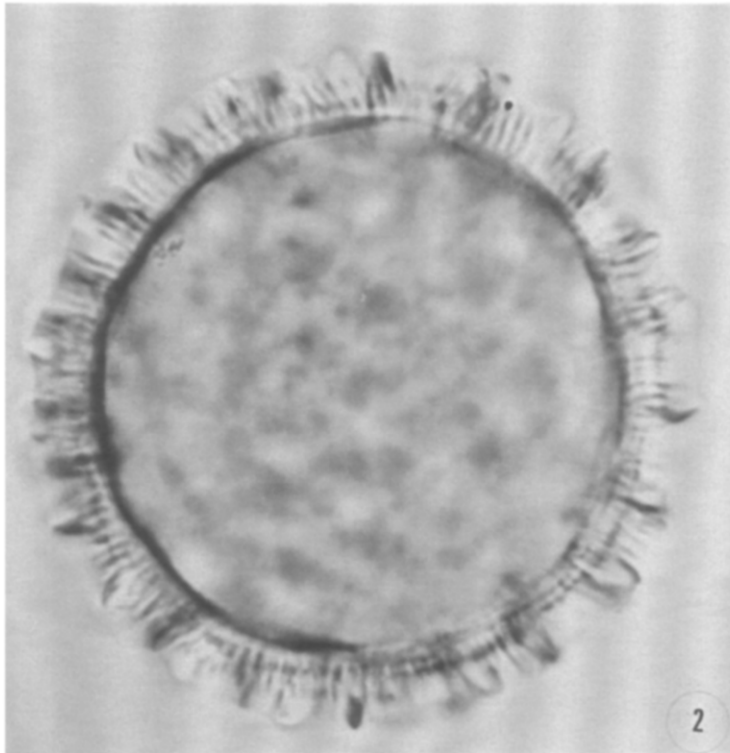
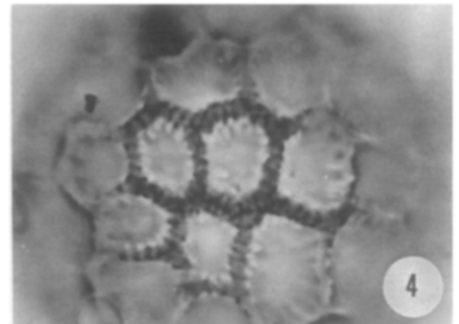
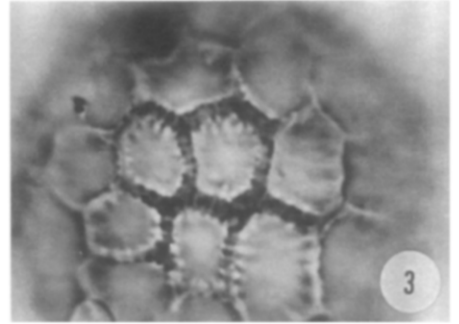
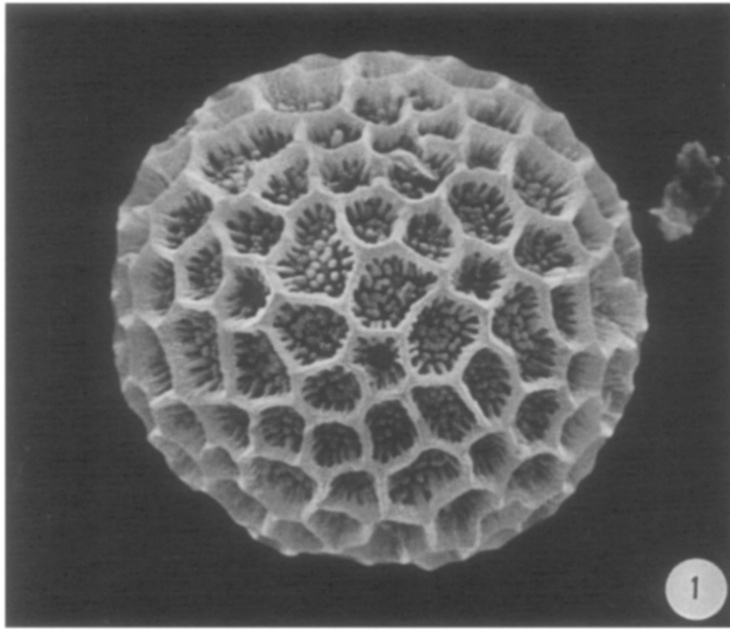


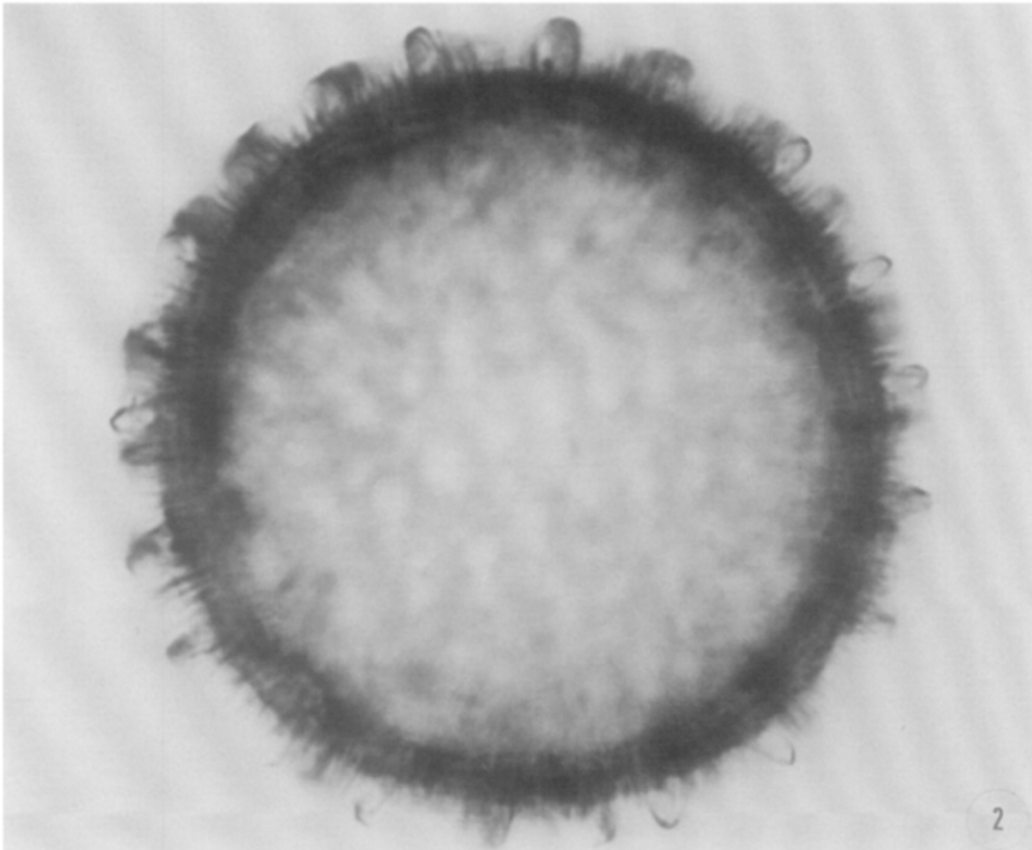
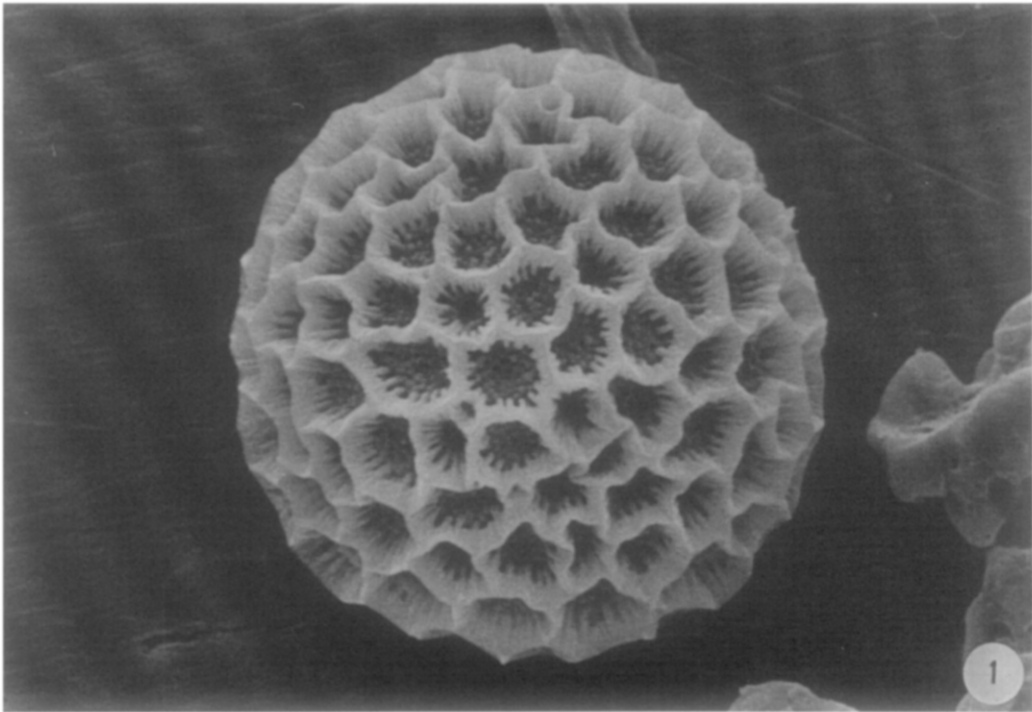
PLATE 22 (*Polygonum persicaria* type: *P. mite*)

PLATE 23 (*Polygonum persicaria* type: *P. mite*)

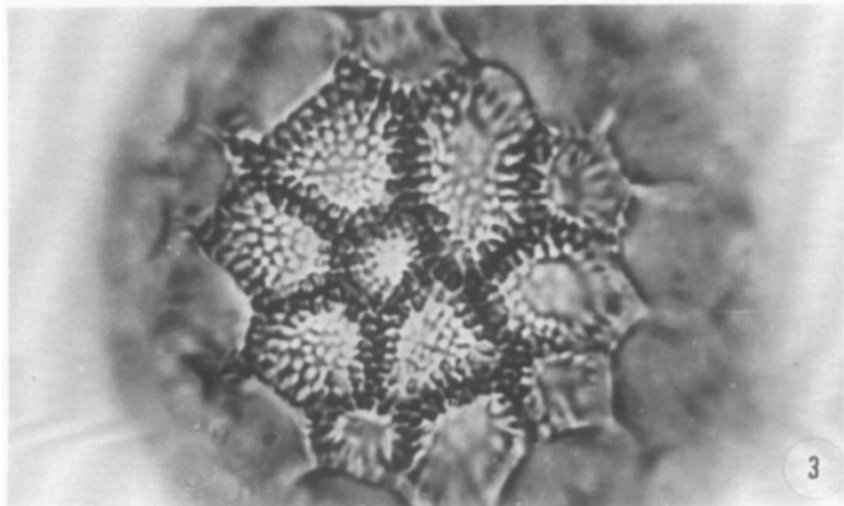
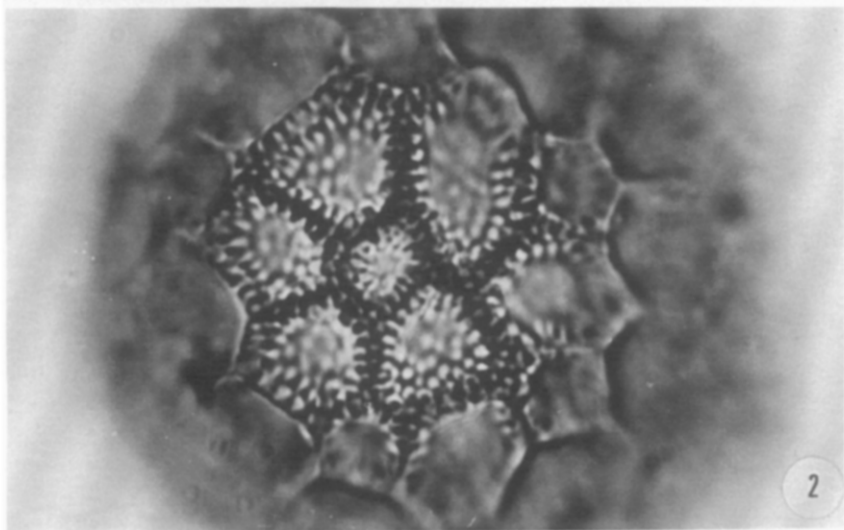
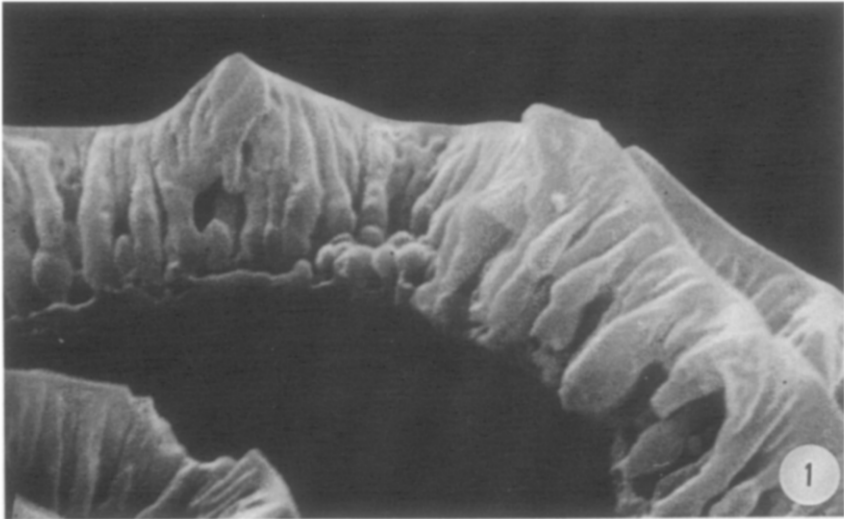


PLATE 24 (p.130)

Polygonum polystachyum Wallich ex Meissner (figs.1–6, De Jongh s.n.)

1. SEM micrograph; oblique view.
2. SEM micrograph; ornamentation ($\times 10,000$).
3. Cross-section.
4. Colpus.
5. Ornamentation, columellae at high focus.
6. Ornamentation, columellae at low focus.

PLATE 25 (p.131)

Rheum officinale L. (figs.1–7, Kok-Ankersmit 10)

1. SEM micrograph; equatorial view.
2. SEM micrograph; polar view.
3. Polar view; cross-section.
4. SEM micrograph; ornamentation ($\times 10,000$).
5. Equatorial view; cross-section.
6. Colpus and ornamentation at high focus.
7. Endocolpus.

PLATE 26 (p.132)

Rheum officinale L. (figs.1–3, Kok-Ankersmit 10)

1. Ornamentation, columellae at high focus.
2. Ornamentation, columellae at medium focus.
3. Ornamentation, columellae at low focus.

Rumex acetosa L. (figs.4–8, Neumann s.n.)

4. SEM micrograph; equatorial view, mesocolpium.
5. SEM micrograph; polar view, 4-colporate grain.
6. SEM micrograph; polar view, 3-colporate grain.
7. SEM micrograph; ornamentation ($\times 10,000$).
8. Equatorial view; cross-section 4-colporate grain.

PLATE 27 (p.133)

Rumex acetosa L. (figs.1–6, Neumann s.n.)

1. Polar view; cross-section, slightly triangular.
2. Polar view; cross-section, circular, colpi not intruding.
3. Polar view; cross-section of 4-colporate grain, colpi not intruding.
4. Polar view; ornamentation at high focus.
5. Polar view; ornamentation at low focus.
6. Endoaperture slightly lalongate, costae endopori interrupted, narrow costae colpi visible.

Oxyria digyna (L.) Hill (figs.7–12, Exc. Biol. Stud. 1970–1926)

7. SEM micrograph; equatorial view.
8. Cross-section of colpi, costae endopori narrow.
9. Equatorial view; cross-section.
10. Polar view; ornamentation at high focus.
11. Polar view; ornamentation at low focus.
12. Polar view; cross-section colpi intruding.

PLATE 28 (p.134)

Oxyria digyna (L.) Hill (figs.1–3, Exc. Biol. Stud. 1970–1926)

1. Colpus at high focus.
2. Colpus at low focus, costae colpi visible.
3. Endoporus, faint costae endopori interrupted.

Rumex acetosella L. (fig.4, White s.n., $2n = 42$; figs.5–6, Den Nijs 508–11, $2n = 28$; figs.7–8, Den Nijs 145–44, $2n = 28$)

4. SEM micrograph; pantocolporate grain ($\times 3000$)
5. SEM micrograph; ornamentation ($\times 10,000$).

(continued on p.135)

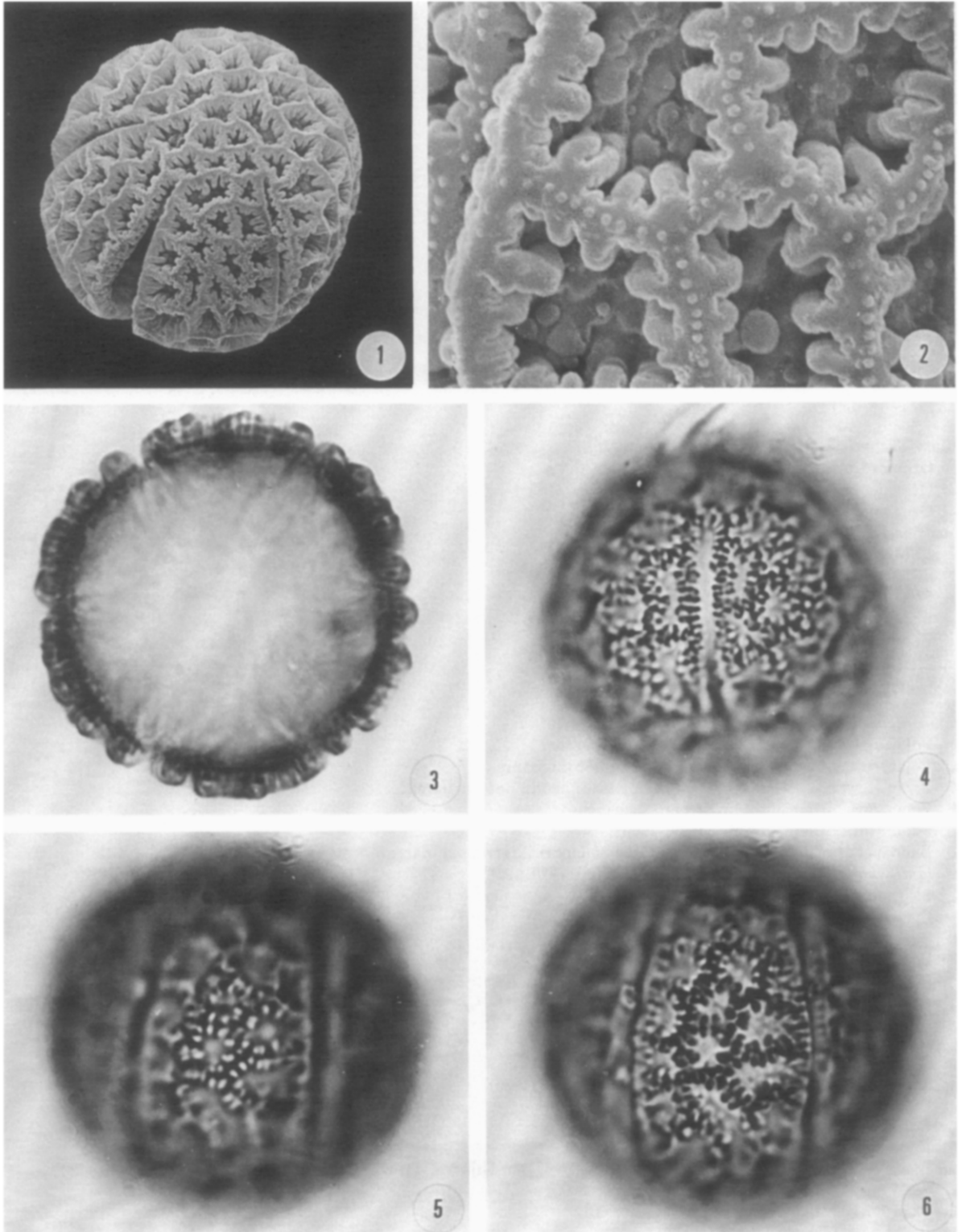
PLATE 24 (*Polygonum polystachyum* type: *P. polystachyum*)

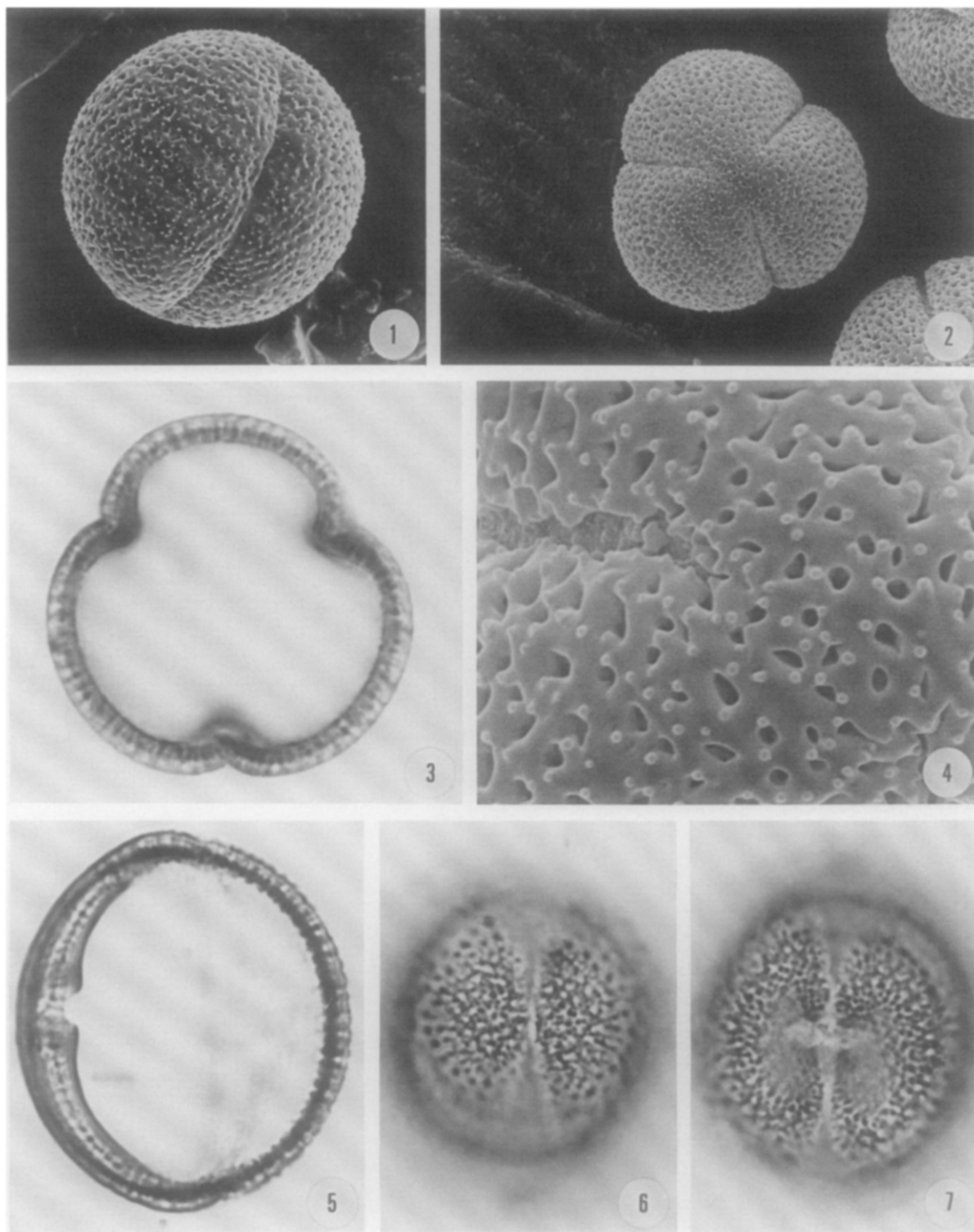
PLATE 25 (*Rheum officinale* type: *R. officinale*)

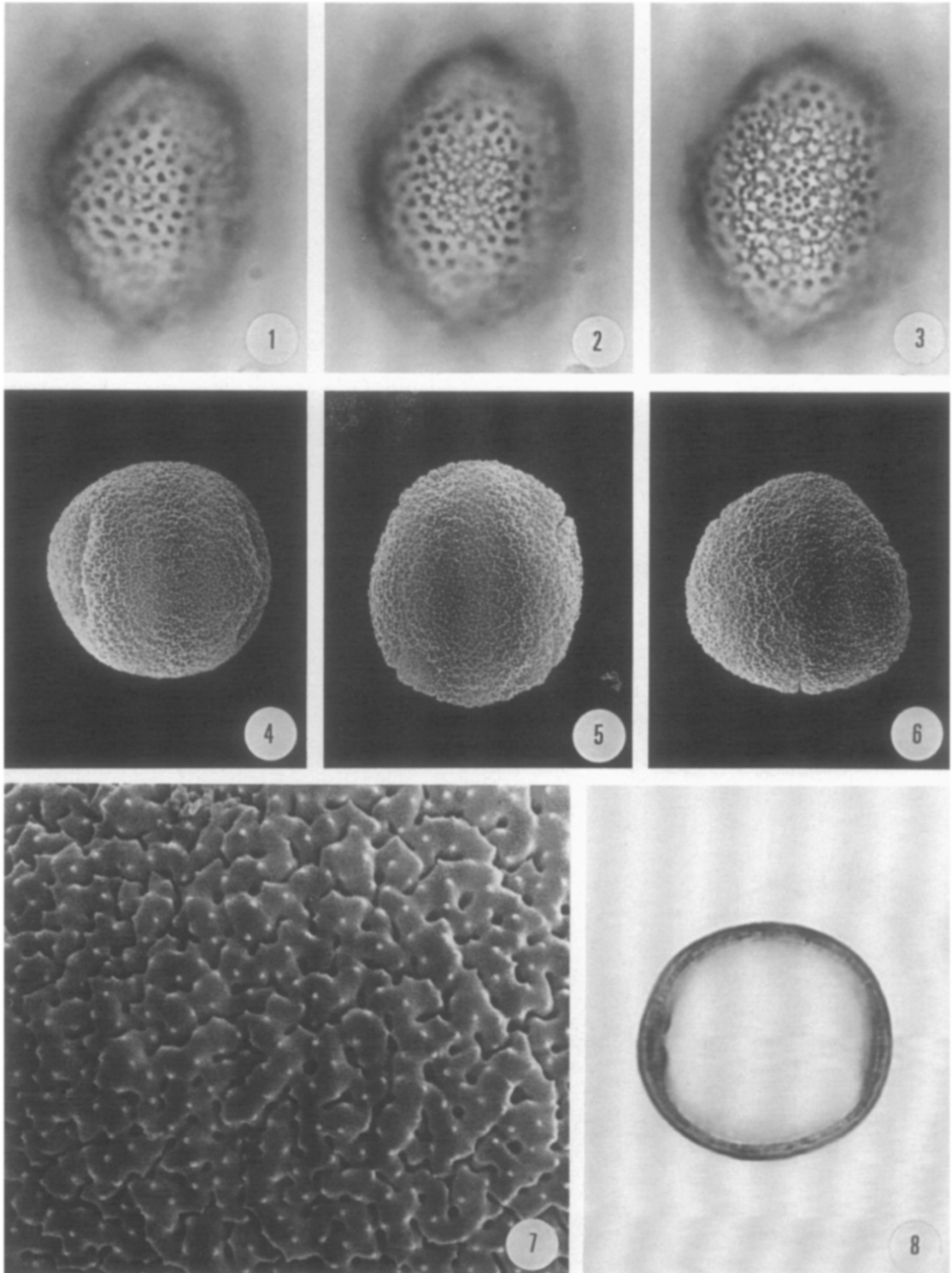
PLATE 26 (*Rheum officinale* type: *R. officinale*, 1–3; *Rumex acetosa* type: *R. acetosa*, 4–8)

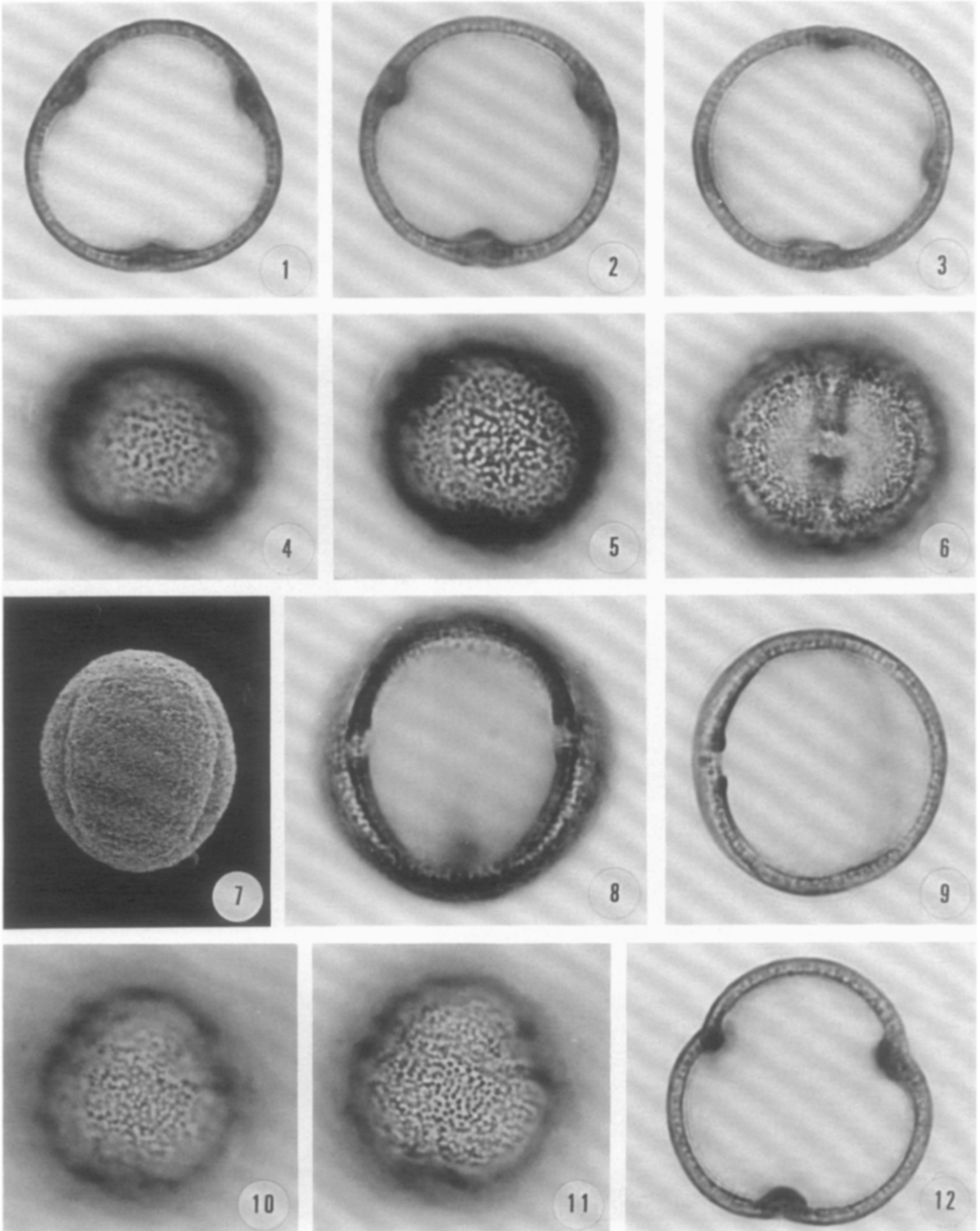
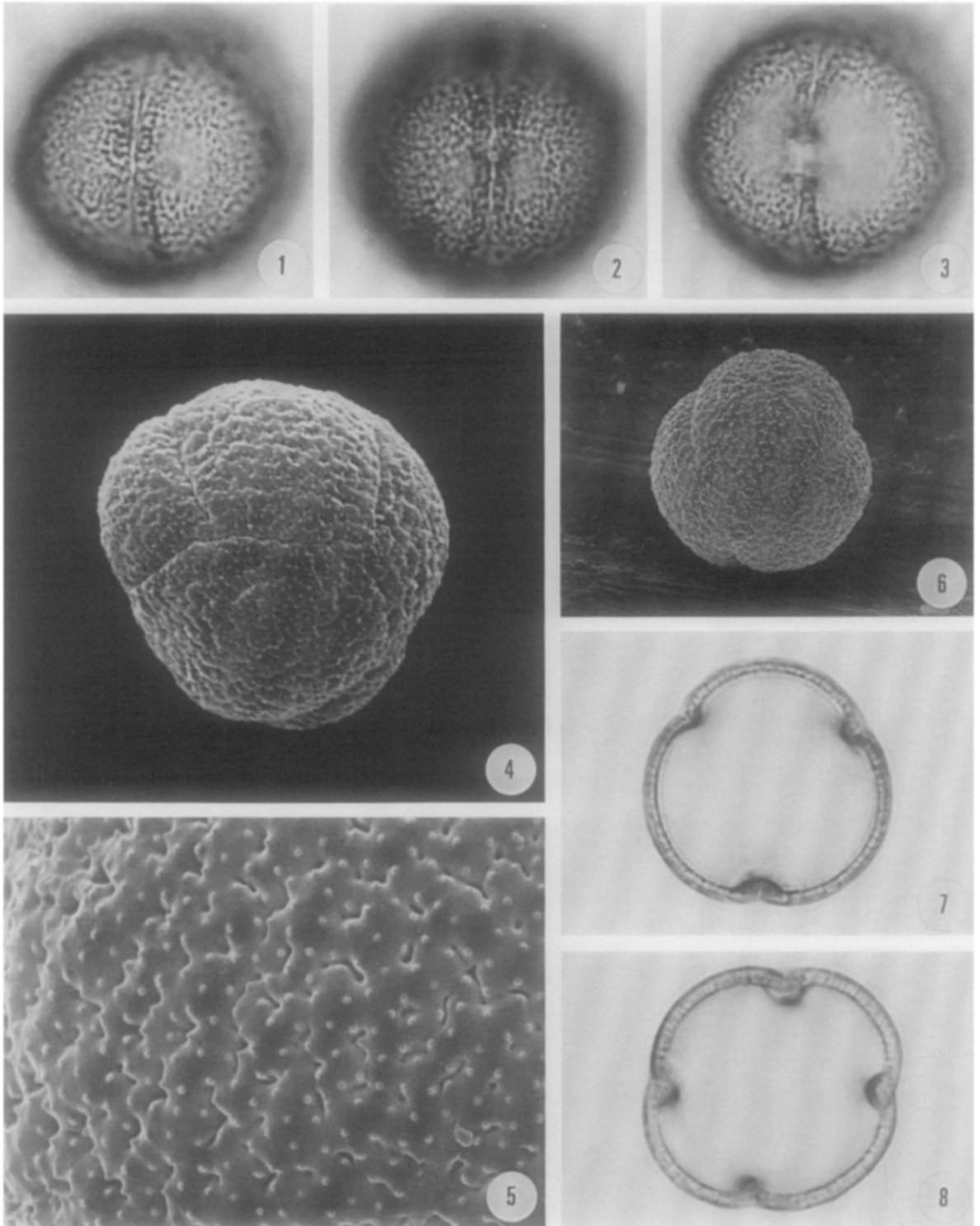
PLATE 27 (*Rumex acetosa* type: *R. acetosa*, 1–6; *Oxyria digyna*, 7–12)

PLATE 28 (*Rumex acetosa* type: *Oxyria digyna*, 1-3; *Rumex acetosella*, 4-8)

6. SEM micrograph; tricolporate grain.
7. Polar view; cross-section 3-colporate grain, colpi intruding.
8. Polar view; cross-section 4-colporate grain, colpi intruding.

PLATE 29 (p.136)

Rumex acetosella L. (fig.1 Den Nijs 121–18, $2n = 14$; figs.2, 3, 5, Den Nijs 145–44, $2n = 28$; fig.4, Den Nijs 106–12, $2n = 14$; fig.6, Den Nijs 100–66, $2n = 42$)

1. Endoaperture, lalongate, costae interrupted.
2. Colpus at high focus, costae colpi.
3. Costae colpi, endoaperture lalongate, costae endopori interrupted.
4. Equatorial view; cross-section.
5. Polar view; 4-colporate grain, ornamentation at low focus.
6. Polar view; 3-colporate grain, ornamentation at low focus.

Rumex alpestris Jacquin (figs.7–9, 11–12, Kintschi 719; fig.10, Exc. Biol. Stud. 1947–805)

7. Ornamentation at high focus.
8. Ornamentation at low focus.
9. Polar view; 4-colporate grain, colpi not intruding.
10. Lolongate, faint endoporus.
11. Equatorial view; cross-section.
12. Polar view; 3-colporate grain, colpi not intruding.

PLATE 30 (p.137)

Rumex aquaticus L. (fig.1, Miquel s.n.; figs.2–7, Buysman 1408)

1. SEM micrograph; whole grain, pantocolporate.
2. SEM micrograph; ornamentation ($\times 10,000$).
3. Cross-section.
4. Lolongate endoporus, faint costae.
5. Ornamentation at high focus.
6. Ornamentation at low focus.
7. Circular endoaperture, faint costae.

PLATE 31 (p.138)

Rumex bucephalophorus L. (figs.1–7, Ten Berge s.n.; fig.8, Cult. Hort. Utrecht 1972–2066)

1. SEM micrograph; polar view.
2. SEM micrograph; ornamentation ($\times 10,000$).
3. Polar view; cross-section.
4. Equatorial view; cross-section, costae endopori narrow but distinct.
5. Ornamentation at low focus.
6. Colpus at high focus.
7. Endoporus, circular and closed.
8. Endoporus, lolongate and closed.

PLATE 32 (p.139)

Rumex conglomeratus Murray (figs.1–5, Exc. Biol. Stud. 1973–20)

1. SEM micrograph; pantoporate grain.
2. Polar view; tricolporate grain, colpi distinctly intruded.
3. Endoporus lolongate, closed.
4. Ornamentation at high focus.
5. Ornamentation at low focus.

Rumex crispus L. (fig.6, Uttien s.n.; fig.7, Mennega s.n.)

6. SEM micrograph; polar view.
7. SEM micrograph; ornamentation ($\times 10,000$).

PLATE 33 (p.140)

Rumex crispus L. (figs.1–5, Mennega s.n.)

1. Polar view; cross-section, colpi slightly intruded.
2. Endoporus; lolongate and closed.

(continued on p.141)

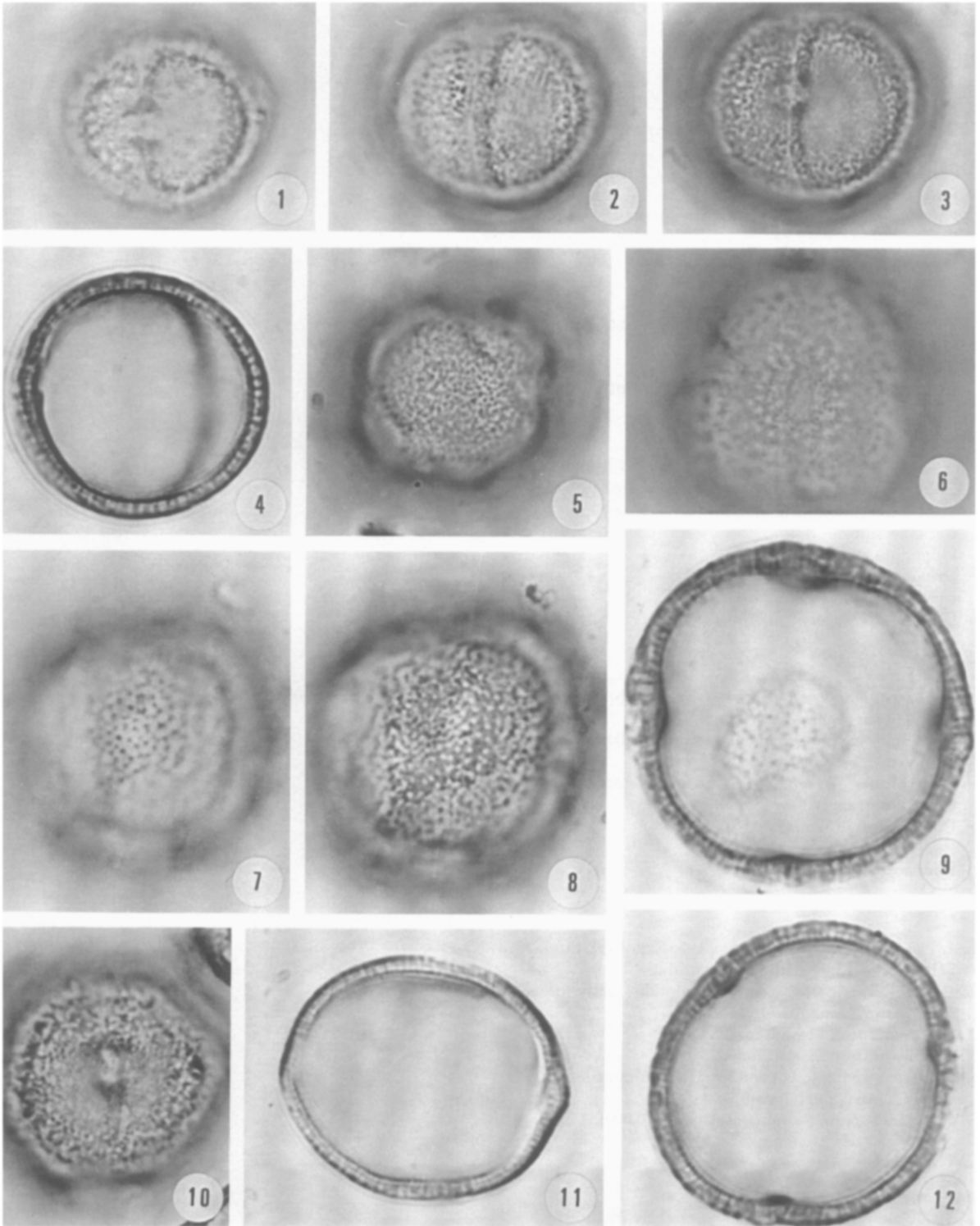
PLATE 29 (*Rumex acetosa* type: *R. acetosella*, 1–6; *R. alpestris*, 7–12)

PLATE 30 (*Rumex acetosa* type: *R. aquaticus*)

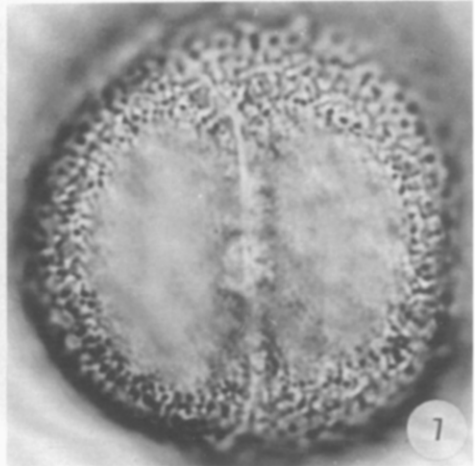
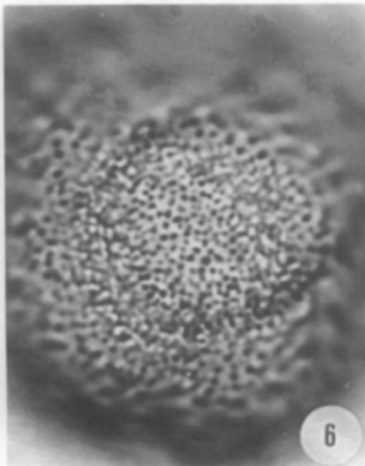
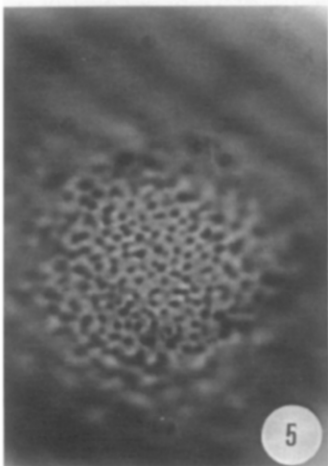
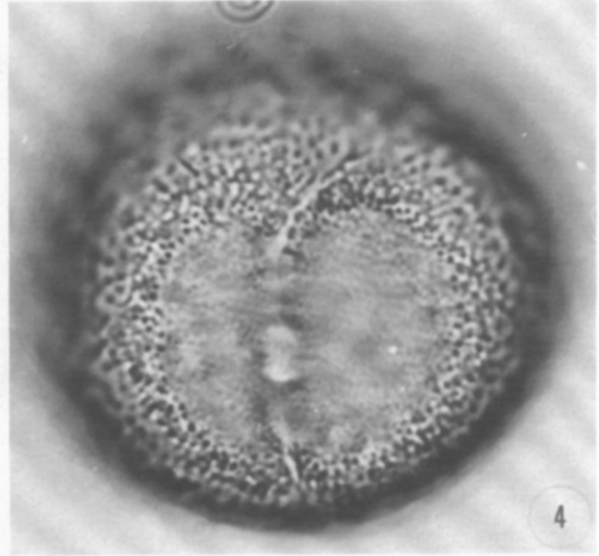
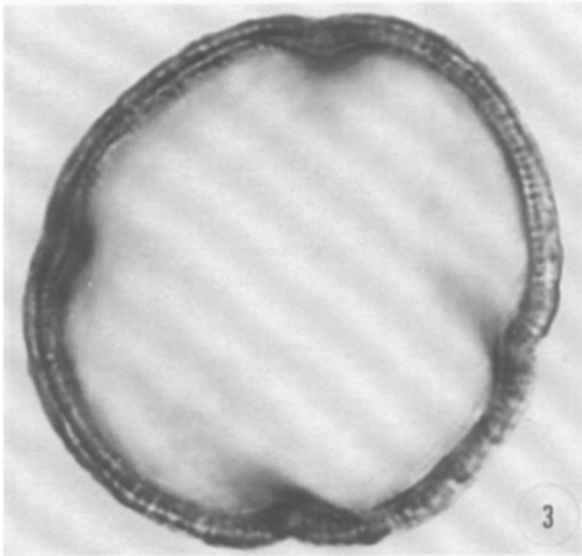
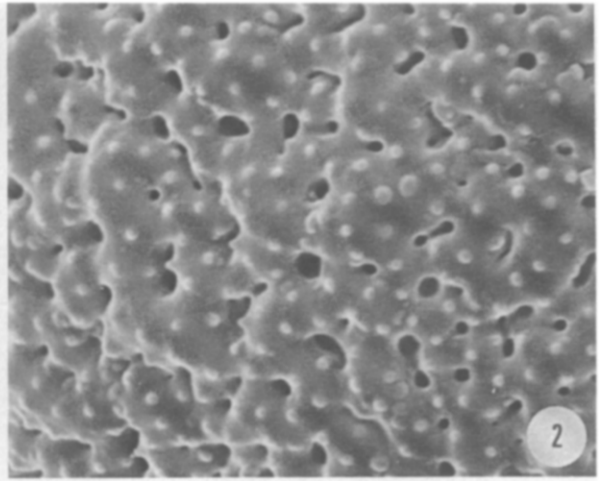
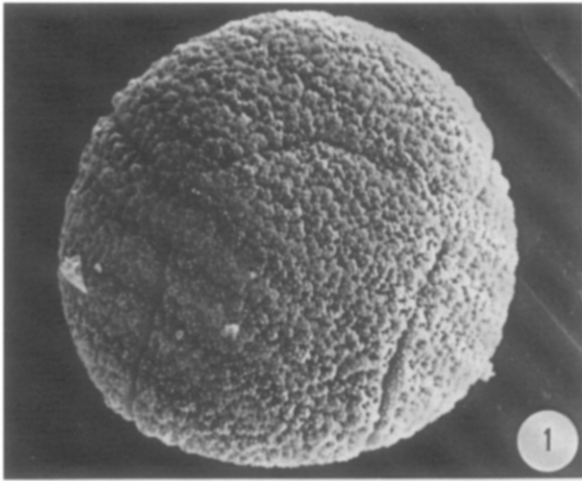


PLATE 31 (*Rumex acetosa* type: *R. bucephalophorus*)

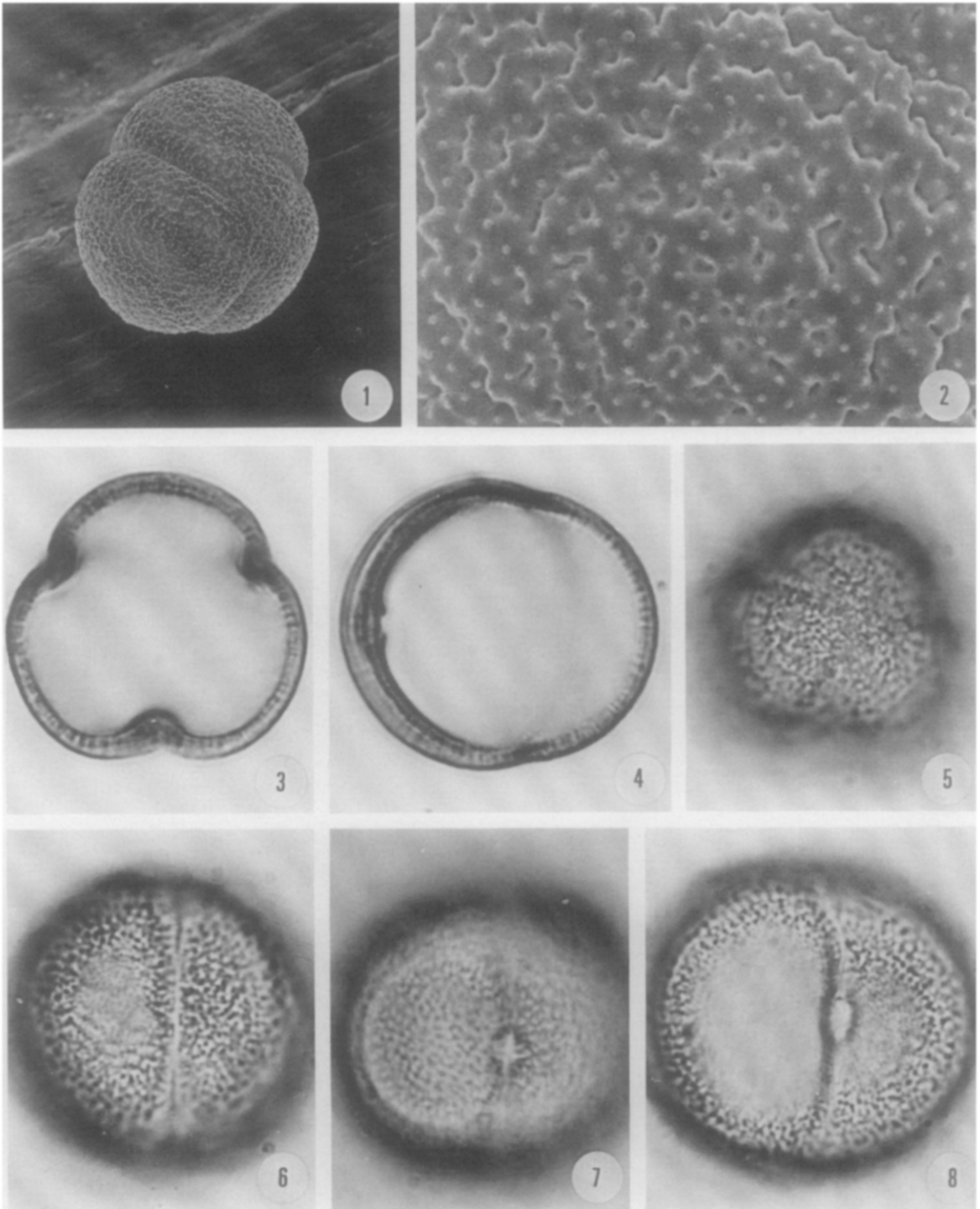


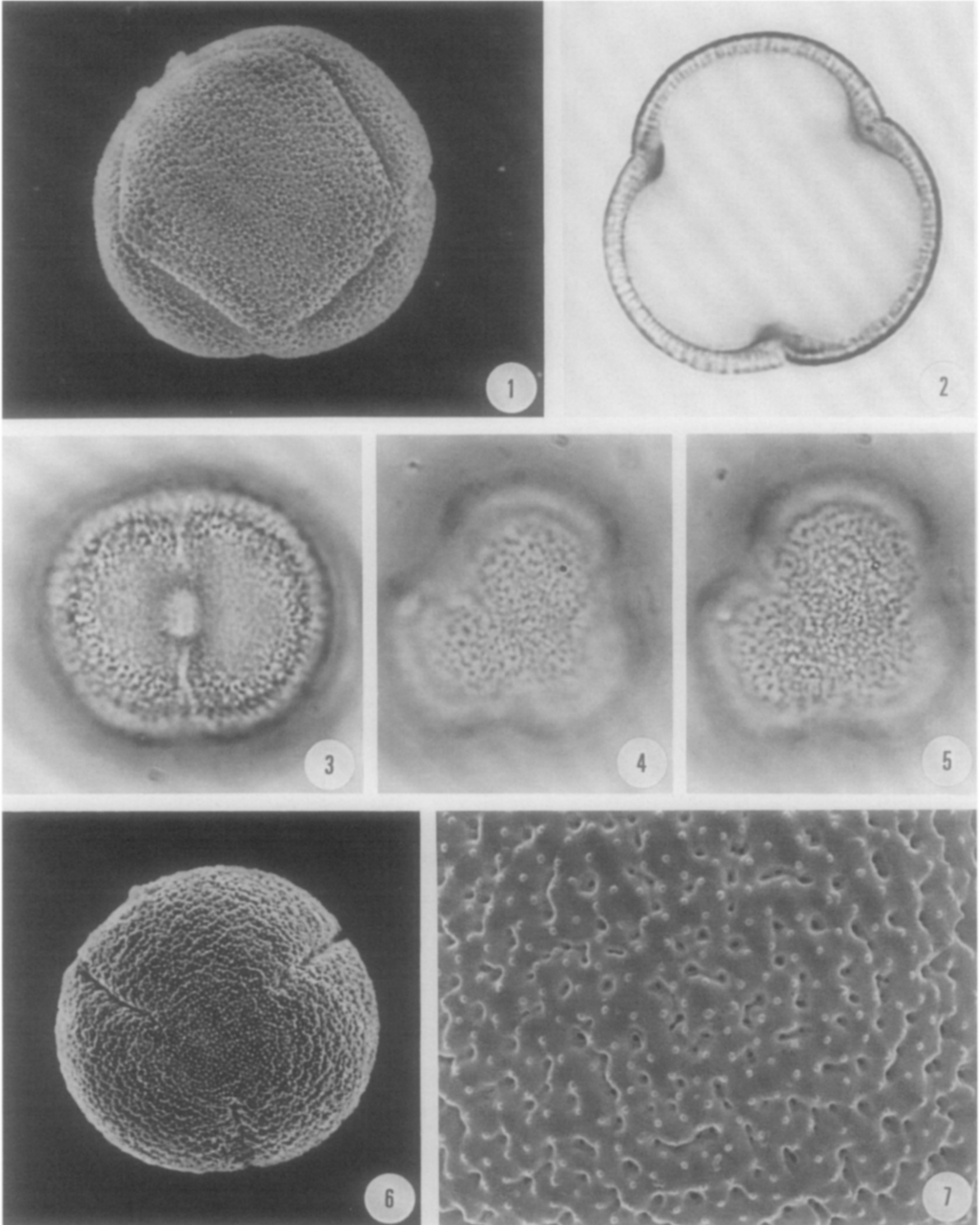
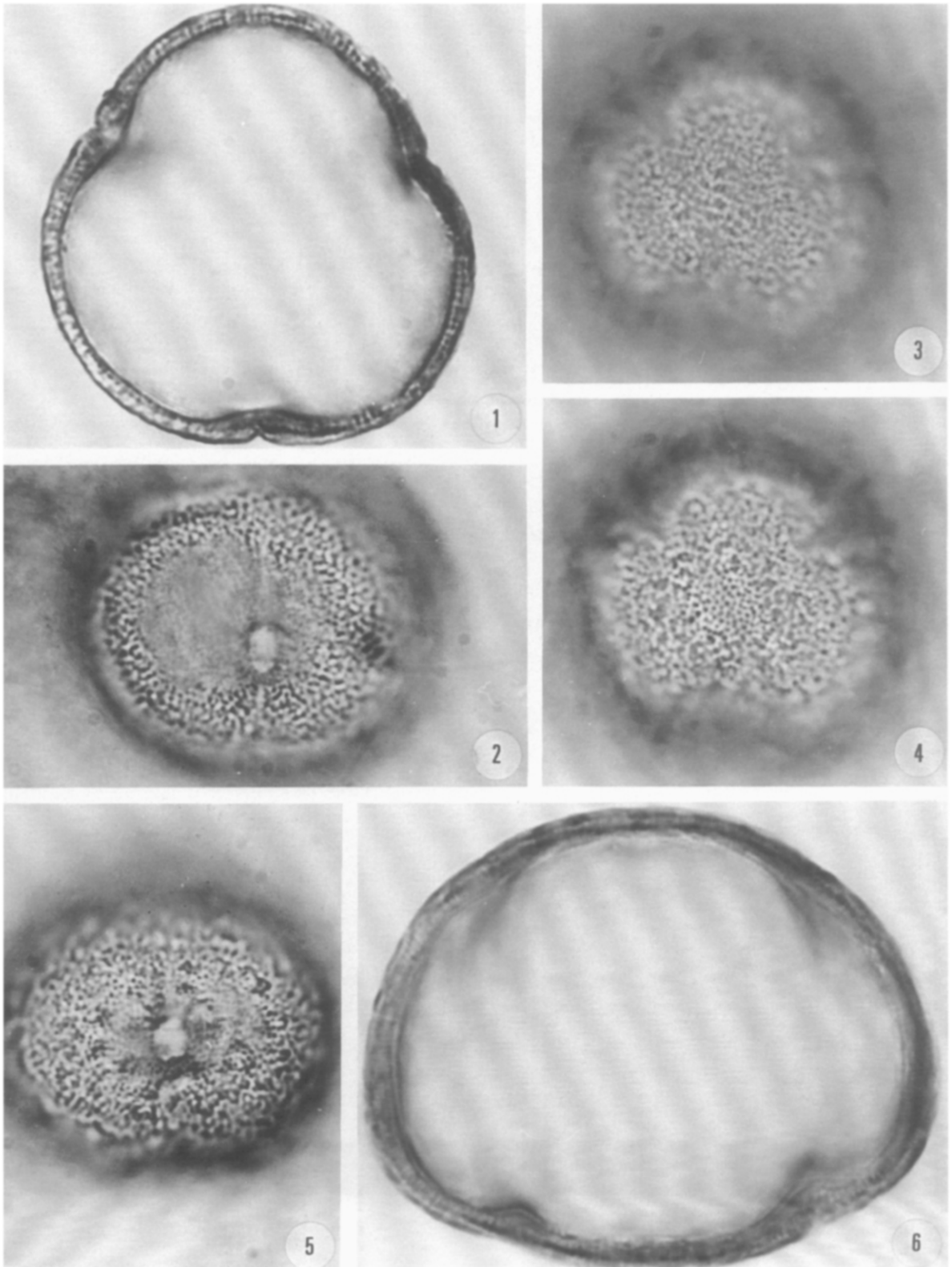
PLATE 32 (*Rumex acetosa* type: *R. conglomeratus*, 1-5; *R. crispus*, 6-7)

PLATE 33 (*Rumex acetosa* type: *R. crispus*, 1-5; *R. hydrolapathum*, 6)



3. Ornamentation at high focus.
 4. Ornamentation at low focus.
 5. Endoporus; circular and closed.
- Rumex hydrolapathum* Hudson (fig.1, Van Royen 363)
6. Cross-section of pantocolporate grain.

PLATE 34 (p.142)

Rumex hydrolapathum Hudson (figs.1-4, 6-7, Punt s.n.; fig.5 Van Royen 363)

1. SEM micrograph; normal pantocolporate grain.
2. SEM micrograph; abnormal grain without apertures.
3. SEM micrograph; tricolporate grain.
4. SEM micrograph; ornamentation ($\times 10,000$).
5. Endoporus; circular and closed.
6. Ornamentation at high focus.
7. Ornamentation at low focus.

PLATE 35 (p.143)

Rumex longifolius Decandolle (figs.1-4, Exc. Biol. Stud. 1965-2097)

1. SEM micrograph; polar view of tricolporate grain.
2. Polar view; cross-section of tricolporate grain, colpi intruded.
3. Endoporus; lolongate and closed.
4. Cross-section of pantocolporate grain.

Rumex maritimus L. (figs.5-6, Colaris 94)

5. SEM micrograph; polar view.
6. Polar view; cross-section, colpi interrupted.

PLATE 36 (p.144)

Rumex maritimus L. (figs.1-3, Colaris 94)

1. Equatorial view; cross-section.
2. Ornamentation at high focus.
3. Ornamentation at low focus.

Rumex obtusifolius L. (fig.4, Behrendsen s.n., figs.5-7, Fresh material Punt; fig.6, Dandy 1253)

4. SEM micrograph; pantocolporate grain.
5. Ornamentation at high focus.
6. Pantocolporate grain; cross-section, colpi not intruded.
7. Ornamentation at low focus.

PLATE 37 (p.145)

Rumex obtusifolius L. (fig.1, Behrendsen s.n.; figs.2-3, Dandy 1253)

1. SEM micrograph; pantocolporate grain ($\times 3000$).
2. Colpus without endoaperture.
3. Costae colpi and endoporus; lolongate and closed.

Rumex palustris L. (figs.5-6, Hekking s.n.)

4. Cross-section of pantocolporate grain.
5. Ornamentation at high focus.
6. Ornamentation at low focus.

PLATE 38 (p.146)

Rumex palustris J. E. Smith (fig.1, Hekking s.n.)

1. Endoporus, circular, closed costae.

Rumex patientia L. (figs.2-8, Exc. K.N.B.V. 1948-6307)

2. Ornamentation at high focus.
3. Ornamentation at low focus.

(continued on p.147)

PLATE 34 (*Rumex acetosa* type: *R. hydrolapathum*)

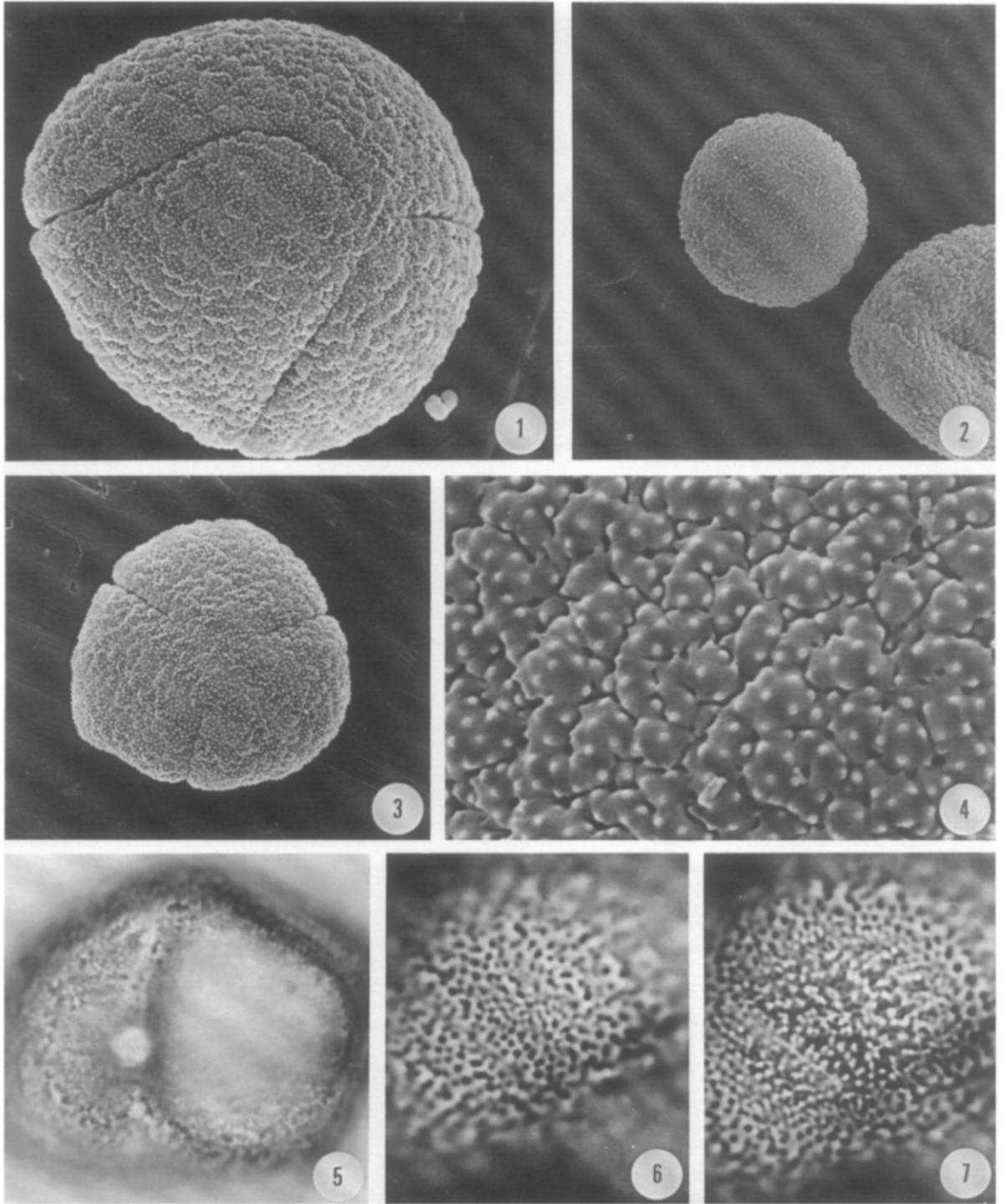


PLATE 35 (*Rumex acetosa* type: *R. longifolius*, 1-4; *R. maritimus*, 5-6)

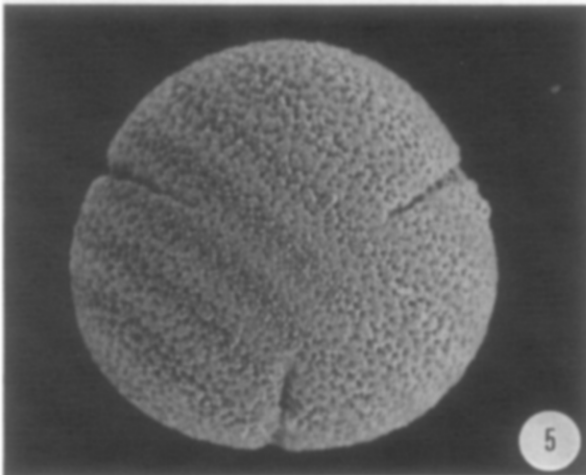
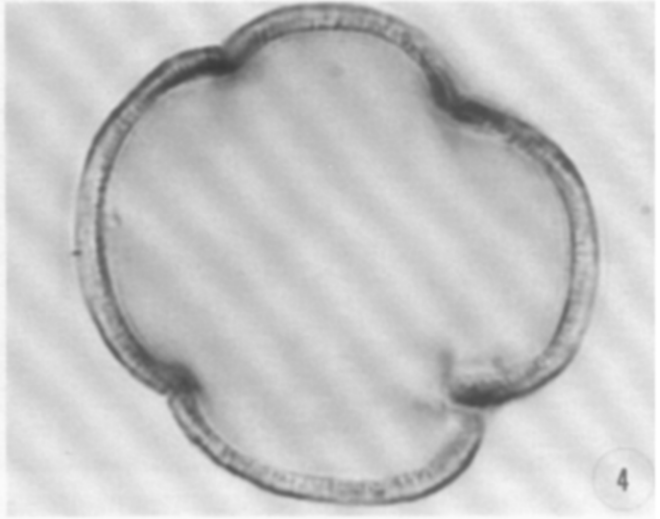
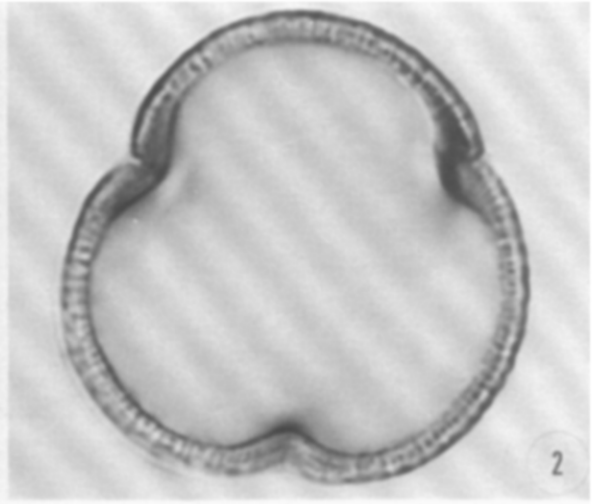
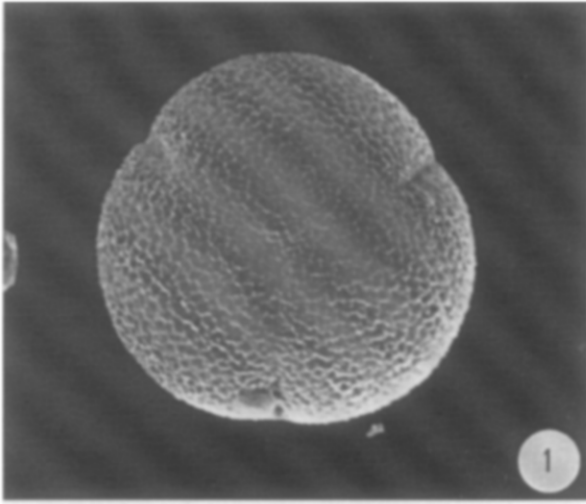


PLATE 36 (*Rumex acetosa* type: *R. maritimus*, 1-3; *R. obtusifolius*, 4-7)

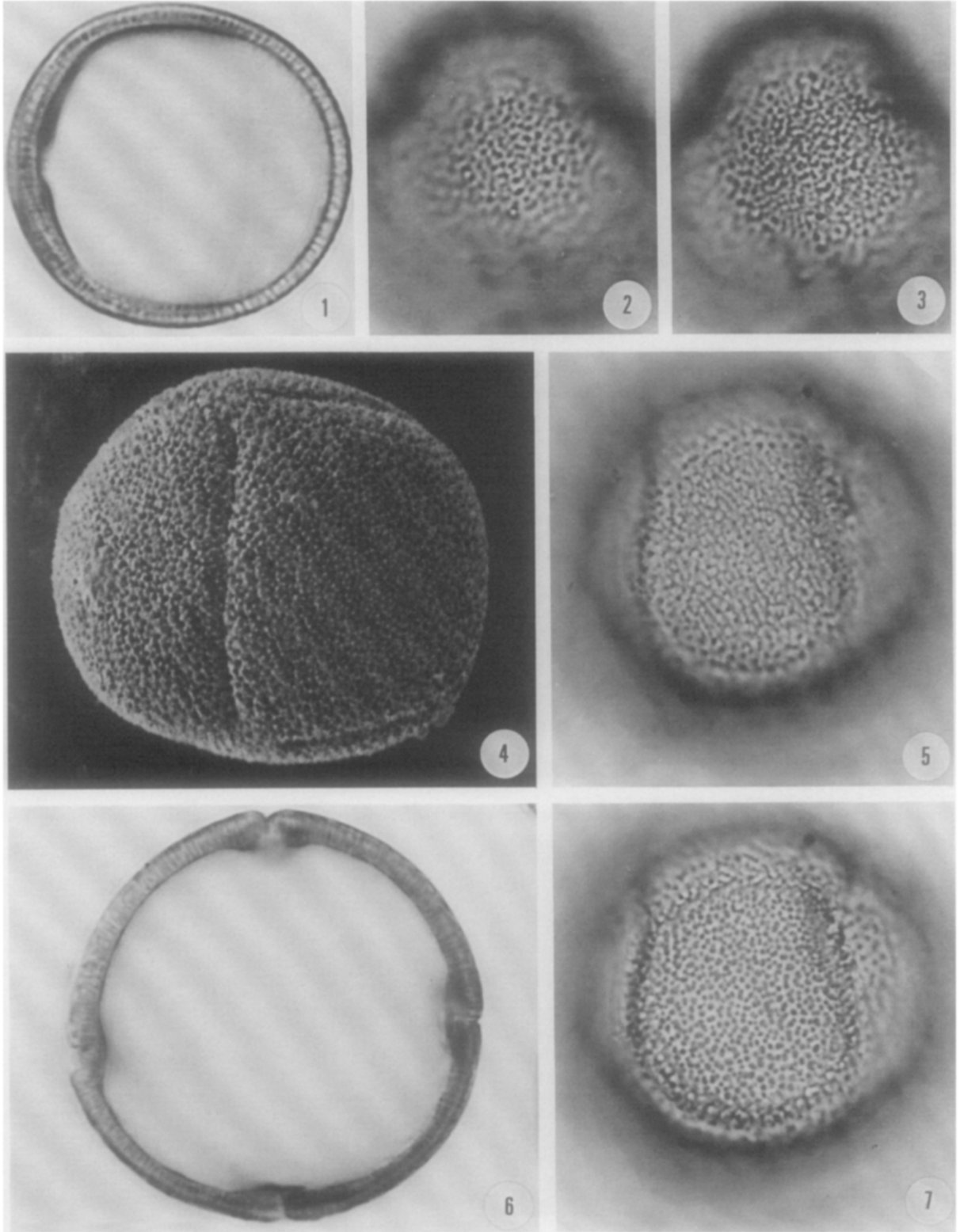


PLATE 37 (*Rumex acetosa* type: *R. obtusifolius*, 1-3; *R. maritimus*, 4; *R. palustris*, 5-6)

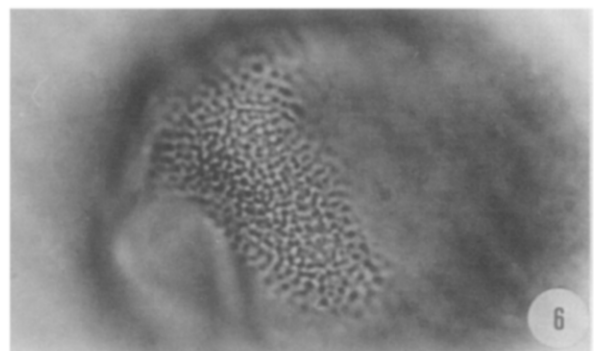
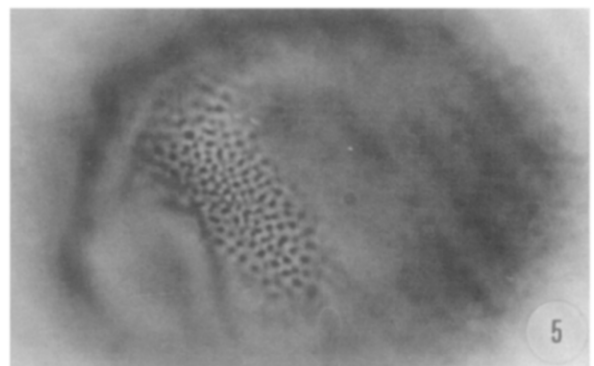
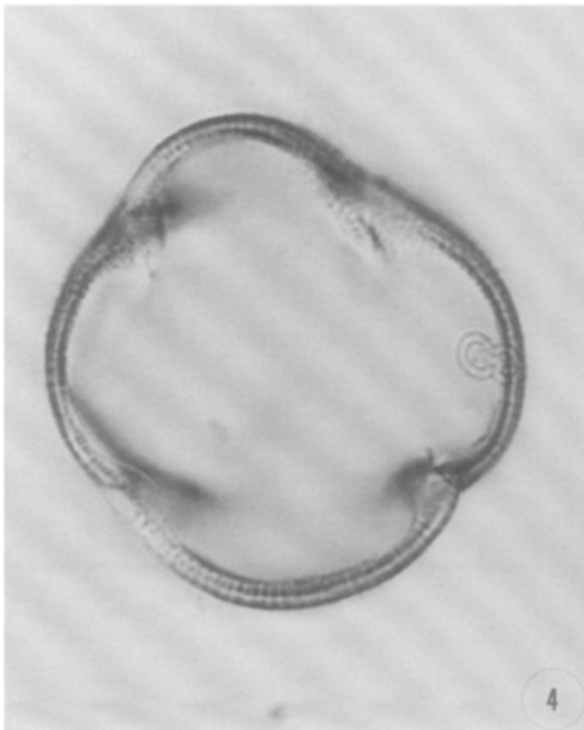
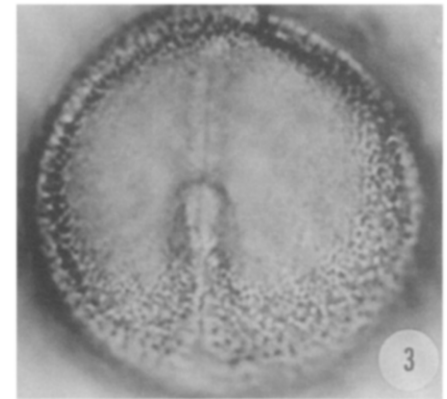
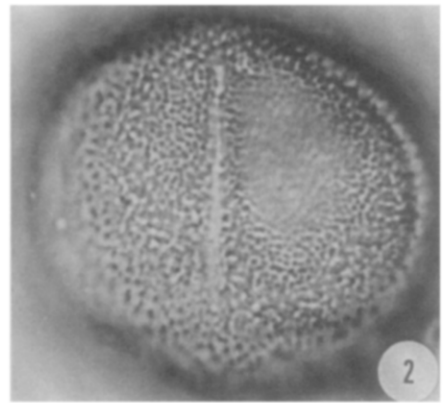
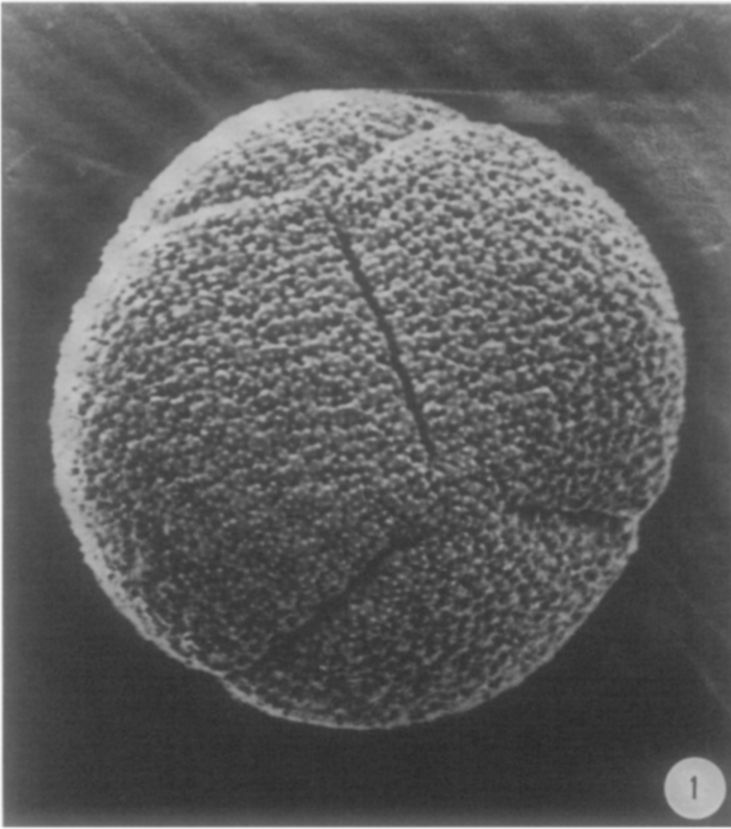
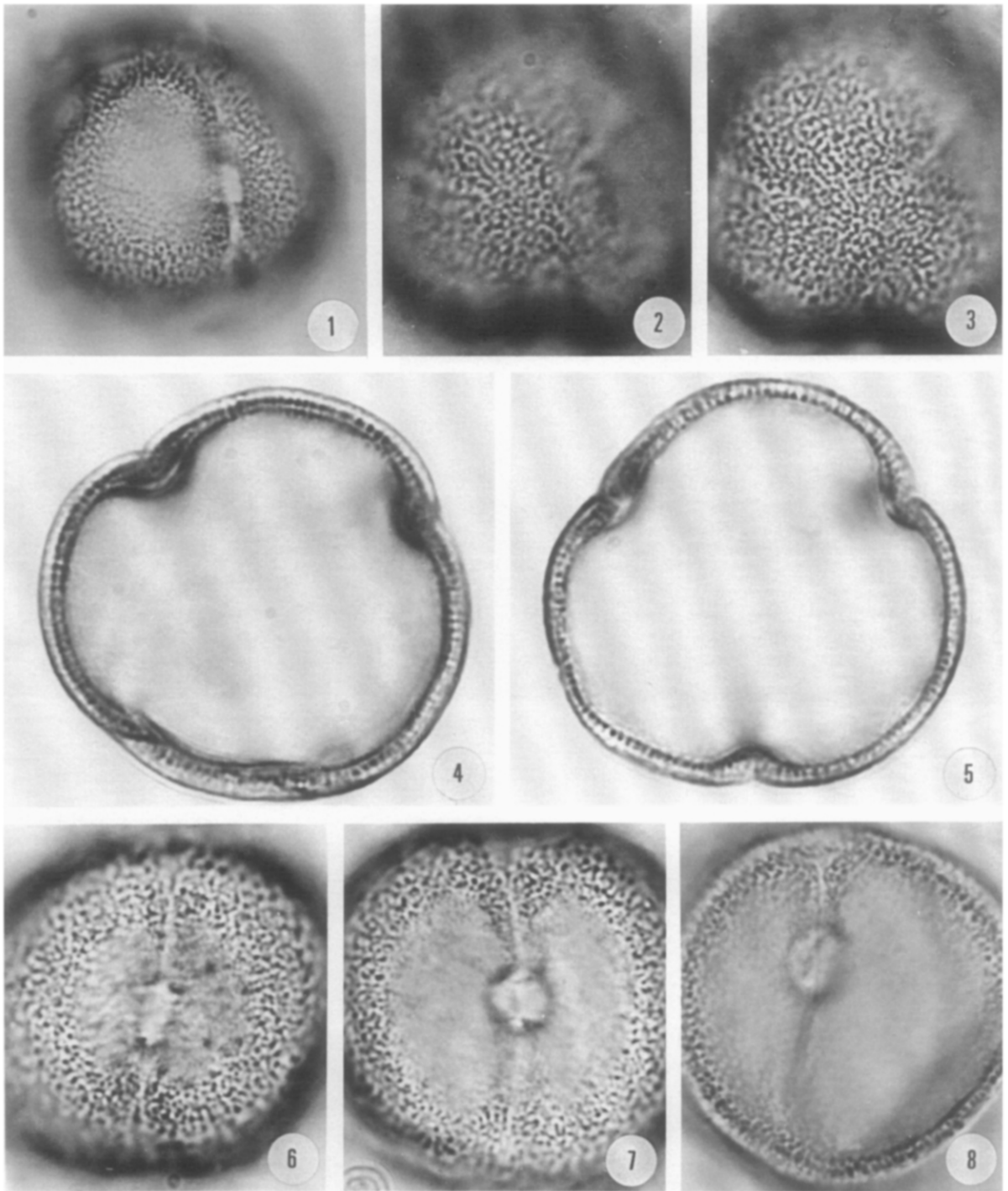


PLATE 38 (*Rumex acetosa* type: *R. palustris*, 1; *R. patientia*, 2-8)

4. Cross-section of pantocolporate grain.
5. Polar view; cross-section of tricolporate grain.
6. Endoporus; lolongate, faint, interrupted costae.
7. Endoporus; circular, with narrow, closed costae.
8. Endoporus, lolongate, faint, closed costae.

PLATE 39 (p.148)

Rumex pulcher L. (figs.1–4, Leeuwenberg 1511)

1. SEM micrograph; equatorial view.
2. SEM micrograph; polar view.
3. Polar view; cross-section, colpi intruded.
4. Endoporus; lolongate with faint, closed costae.

Rumex rupestris Le Gall (figs.5–6, Danser, s.n.)

5. Polar view, cross-section, colpi intruded.
6. Endoporus; circular, distinct, closed costae.

PLATE 40 (p.149)

Rumex sanguineus L. (figs.1–5, Exc. Biol. Stud. 1973–30)

1. SEM micrograph; equatorial view of tricolporate grain.
2. SEM micrograph; pantocolporate grain.
3. Ornamentation at low focus.
4. Polar view; cross-section, colpi intruded.
5. Endoporus; circular and closed.

Rumex scutatus L. (figs.6–10, Rutten s.n.)

6. Polar view; cross-section, colpi intruded.
7. Equatorial view; cross-section.
8. Endoporus; circular, faint costae just closed.
9. Endoporus; lolongate, closed costae.
10. Colpus at low focus, costae colpi.

PLATE 41 (p.150)

Rumex thyrsoiflorus Fingerhuth (figs.1–5, Jansen en Wachter 6173; 6–8, Boom 17477)

1. SEM micrograph; polar view ($\times 3000$).
2. SEM micrograph; ornamentation ($\times 10,000$).
3. Polar view; cross-section of tricolporate grain, colpi only slightly intruded.
4. Polar view; cross-section of 4-colporate grain.
5. Equatorial view; cross-section.
6. Ornamentation at high focus.
7. Ornamentation at low focus.
8. Endoporus; lolongate, closed costae.

PLATE 42 (p.151)

Rumex triangulivalvis (Danser) Rechinger (fig.1, Bakhuizen vd. Brink 4565; figs.2–6, Kern 4733)

1. SEM micrograph; polar view.
2. Endoporus; lolongate, closed costae.
3. Polar view; cross-section, colpi not intruded.
4. Ornamentation at high focus.
5. Equatorial view; cross-section.
6. Ornamentation at low focus.

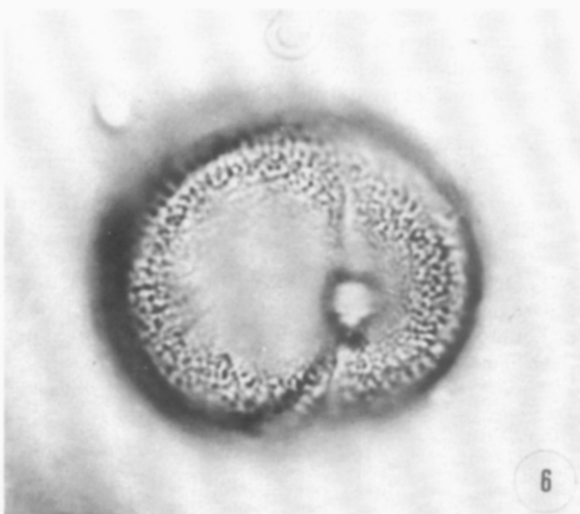
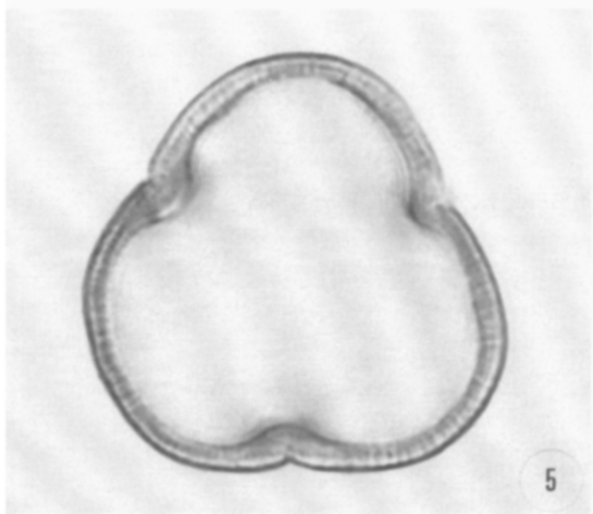
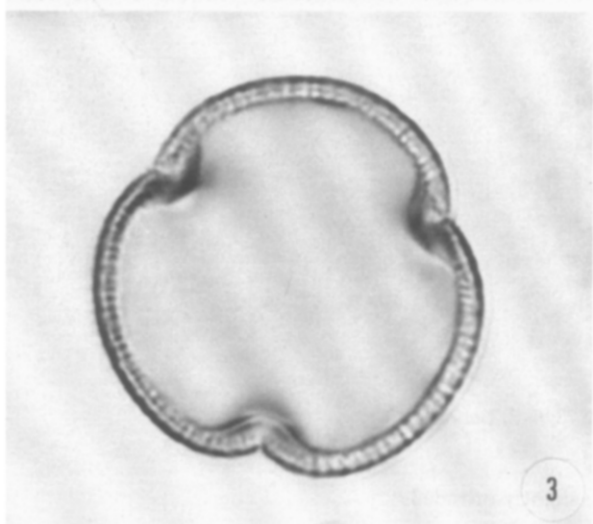
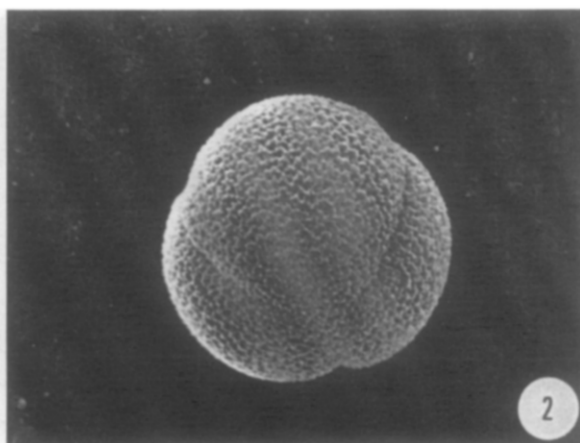
PLATE 39 (*Rumex acetosa* type: *R. pulcher*, 1-4; *R. rupestris* 5-6)

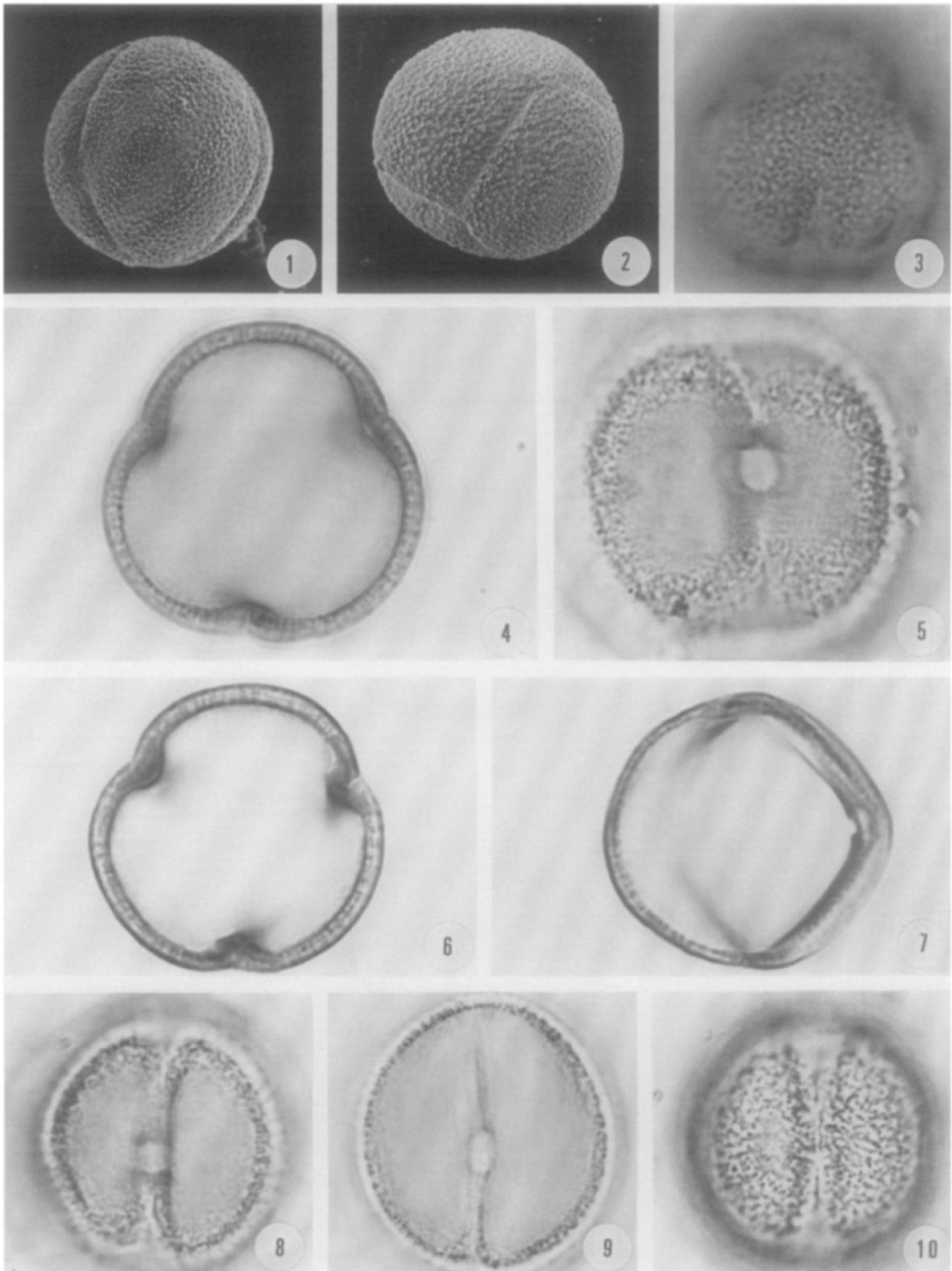
PLATE 40 (*Rumex acetosa* type: *R. sanguineus*, 1-5; *R. scutatus* 6-10)

PLATE 41 (*Rumex acetosa* type: *R. thyrsiflorus*)

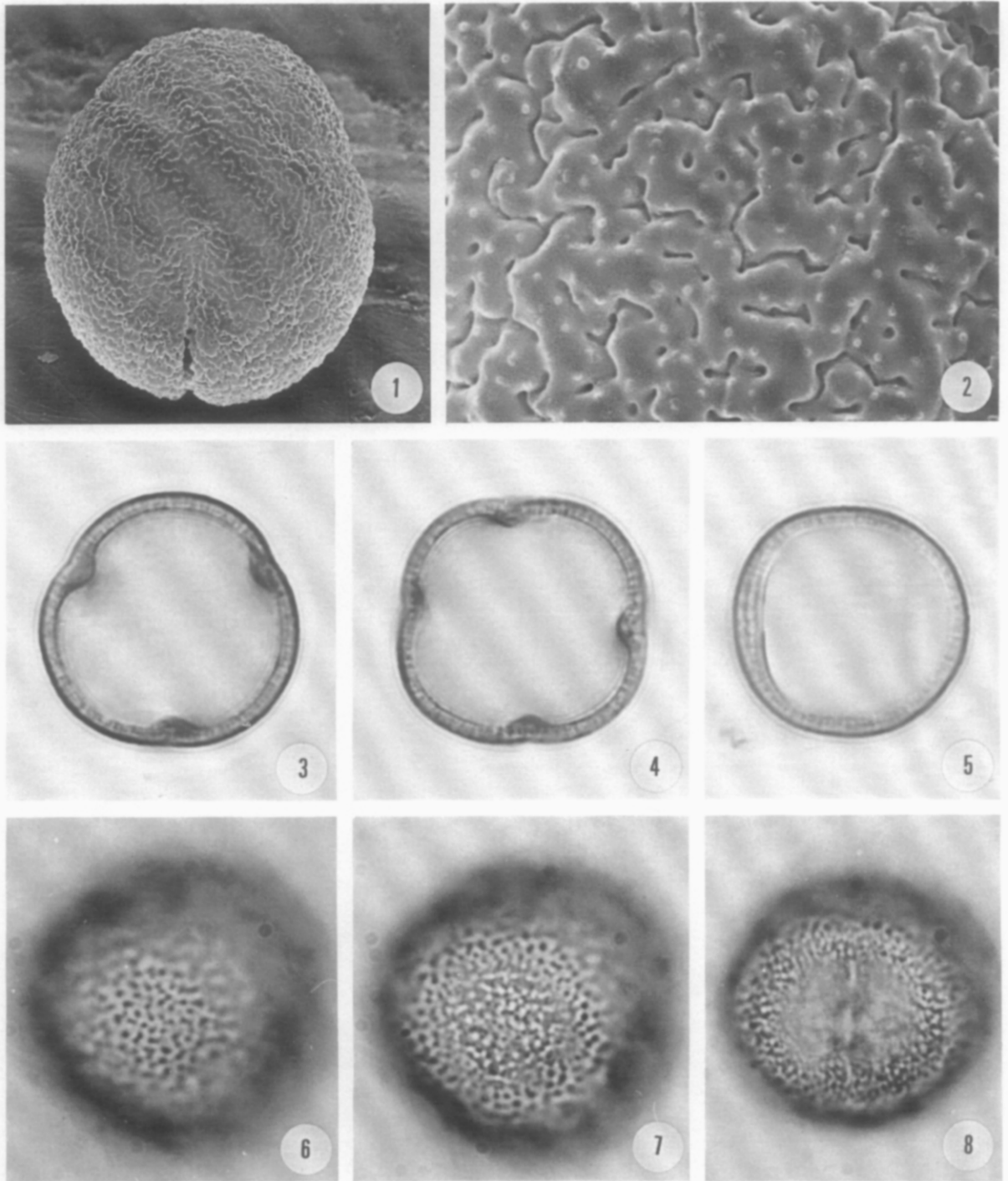


PLATE 42 (*Rumex acetosa* type: *R. triangulivalvis*)