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POLLEN MORPHOLOGY OF THE STEMONACEAE

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SUMMARY

A pollen-morphological survey of all four genera of the Stemonaceae at the light and electron microscope level is presented. Stemonaceae is a eurypalynous family. *Stichoneuron* pollen, up to now described as monosulcate, appears to be inaperturate. *Pentastemona* pollen is most deviating in Stemonaceae. Its sexine consists of elements that resemble Ubisch bodies very much. It shares several features with pollen of *Peliosanthes* (Convallariaceae) and *Trillium* (Trilliaceae). However, the closest relatives of *Pentastemona* could not be traced with the available pollen-morphological evidence.

INTRODUCTION

The family Stemonaceae includes four genera: *Croomia, Pentastemona, Stemona,* and *Stichoneuron,* which occur in S and E Asia, N Australia and SE North America. *Pentastemona* was described by Van Steenis (1982) as the first monocot genus known to have regular 5-merous flowers. It possesses several other characters not shared with the other Stemonaceae. Actually the other three genera are mutually rather different too. According to Tomlinson & Ayensu (1968) they evidently do not form a natural assemblage (many differences, few similarities), and it is clear that *Pentastemona* does not fill any of the gaps. However, being more impressed by the few characters shared by all four genera rather than by the many differences Van Steenis (1982) recognised them as a natural family, favouring affinity with the Dioscoreaceae. The shared features included the vegetative morphology and anatomy, the anatropous ovules, the 1-celled ovary, and seed structure. The pollen of all four genera had been studied as well, but it did not provide features that support the naturalness of the family. Rather it stressed its heterogeneity. *Pentastemona* pollen was found to be most deviating.

The relationships within the Stemonaceae were questioned again during the taxonomic research in the framework of the Flora Malesiana project (Duyfjes, 1992, in prep.). Once more *Pentastemona* appeared to be aberrant. Its peculiarities would justify ranking at family level. As the available pollen-morphological evidence is rather inconclusive up to now, being based on a few LM observations only (see below), a detailed study was undertaken in order to provide a more extensive basis for taxonomic decisions, especially with respect to the position of *Pentastemona.* Concurrently an investigation into flower morphology was carried out (Van Heel, 1992, in prep.).

Literature of Stemonaceae pollen

Stemonaceae pollen has been given little attention up to now. Nearly all reports are based on LM data, and include only one or a few species:

Erdtman (1952):	*Croomia japonica, Stemona mairei*
Ikuse (1956):	*Croomia heterosepala, Stemona japonica, S. sessilifolia*
Huang (1970, 1972):	*Stemona tuberosa*
Rogers (1982):	*Croomia*
Van Steenis (1982):	*Croomia (japonica), Pentastemona egregia, P. sumatrana, Stemona australiana, S. gloriosa, S. japonica, S. tuberosa, Stichoneuron (caudatum)*
Zavada (1983):	*Croomia, Stemona japonica, Stichoneuron*

Zavada (1983) presented a few scanning and transmission electron micrographs of *Stemona japonica* pollen; he noted that the infratectal layer was "reminiscent of the alveolar walls of some fossil pteridosperms and extant cycads."

The account of Van Steenis (1982) was based on an LM survey by J. Muller (made in 1975). The aperture type was described as monosulcate in *Croomia, Stemona* and *Stichoneuron,* and as inaperturate in *Pentastemona.* The exine was found to be reticulate in *Croomia* and *Stichoneuron,* very thin and densely covered by minute granules in *Pentastemona,* finely structured in *Stemona australiana, S. japonica* and *S. tuberosa,* and thinly columellate in *S. gloriosa.* Resemblance of *Pentastemona* pollen with that of Araceae-Philodendroideae was mentioned.

MATERIAL AND METHODS

The genus *Croomia* consists of three species: one in the southeastern United States and two in Japan and China (Rogers, 1982). *Pentastemona* has two species, which are both limited to Sumatra (Van Steenis, 1982). The number of species reported for *Stemona* is from 25 (Dahlgren et al., 1985) to c. 30 (Rogers, 1982). However, after monographic revision probably not more than 15 to 20 species will remain (personal comm. B.E.E. Duyfjes). The distribution of *Stemona* extends from Sri Lanka and E India to Japan, and southwards through Malesia to N Australia. The two species of *Stichoneuron* occur in Bangladesh and Assam, and near the border between Malaysia and Thailand.

The collections sampled for the present pollen-morphological study are listed below.

Croomia Torrey & Gray

C. japonica Miq. – Japan: L sheets 908.225-1340[1], -1376, -1377[1, 2, 4].
C. pauciflora (Nutt.) Torrey & Gray – Botanic Garden München: *Bogner 1861*[1, 3, 4].

Pentastemona Steen.

P. egregia (Schott) Steen. – Botanic Garden München: *Bogner 1724*[1, 3, 4] – Sumatra: *Meijer 17010*[1, 2].
P. sumatrana Steen. – Sumatra: *de Wilde & de Wilde-Duyfjes 20311*[1, 3], *21399*[3, 5].

Stemona Lour.

S. australiana (Benth.) C.H. Wright – Australia: *Wightman 1063*[3] (DNA) – New Guinea: *Brass 8739*[1], *Versteeg 1913*[4].
S. cochinchinensis Gagnep. – Thailand: *Kerr 21335*[1, 2], *Lakshnakara 959*[1].
S. collinsae Craib – Thailand: *Maxwell 75-94*[1].
S. curtisii Hook. f. – Thailand: *Maxwell 87-389*[1, 4].
S. japonica (Bl.) Franch. & Sav. – Japan: *d'Alleizette 7353*[1, 2, 4], *Makino 71842*[1, 4].
S. javanica (Kunth) Engler – Java: *Backer 17353*[1].
S. kerrii Craib – Thailand: *BKF 32037*[3], *Larsen, Santisuk & Warncke 2351*[1, 2].
S. lucida (R. Br.) Duyfjes – New Guinea: *NGF 19108*[1, 2, 4].
S. parviflora C.H. Wright – Hainan: *Ford 412*[1] (K).
S. phyllantha Gagnepain – Thailand: *Kerr 20687*[1].
S. prostrata Telford – Australia: *Byrnes 2071*[1, 2].
S. sessilifolia (Miq.) Franch. & Sav. – Japan: L sheet 908.225-1397[1].
S. tuberosa Lour. var. *ternatensis* (J.J. Smith) Duyfjes – Ambon: *Robinson 295*[1, 4] – Timor: *Treub 1893*; var. *tuberosa* – Botanic Garden München: *Bogner s.n.*[1, 2, 3].
S. wardii W.W. Smith – China: *Delavay 1835*[1, 3].

Stichoneuron Hook. f.

S. caudatum Ridley – Botanic Garden München: *Bogner 1789*[1, 2, 3, 4] – Malay Peninsula: *Stone & Sidek 12514*.
S. membranaceum Hook. f. – India: *Koelz 5835*[1].

Acetolysed pollen of all collections except *de Wilde & de Wilde-Duyfjes 21399* (*Pentastemona sumatrana*), *Wightman 1063* (*Stemona australiana*) and *BKF 32037* (*Stemona kerrii*) was studied with LM. The superscript numbers refer to various other techniques applied:

1 = acetolysed pollen studied with SEM
2 = sectioned acetolysed pollen studied with SEM
3 = unacetolysed critical point dried pollen studied with SEM
4 = unacetolysed pollen studied with TEM
5 = unacetolysed pollen studied with LM

The collections from the Botanic Garden at München were represented as fluid-preserved flowers and buds. The rest is dried material, kept in the Rijksherbarium, Leiden (L) unless indicated otherwise.

Techniques

Acetolysis was carried out according to the Erdtman-method (with minor amendments; see Van der Ham, 1990).

For SEM the material was coated with gold using a Polaron E 5100 II sputter-coater. Sections were made with a Leitz freezing microtome according to Muller (1973). Critical point drying was carried out with a Polaron E 3000 critical point dryer, using dimethoxymethane and CO_2.

Preparation for TEM included rehydration with Triton of the herbarium material (1 week, 4°C), and for all material fixation with 1% OsO_4 (1.5 hour), prestaining with 1% uranylacetate during dehydration, embedding in 3/7 Epon, poststaining with uranylacetate (7 minutes) and Reynolds' lead citrate (5 minutes), and sectioning with a diamond knife on an LKB Ultratome III.

Measurements

The exine of Stemonaceae pollen appeared to be very susceptible to collapse. This is due to its relatively thin nexine (compared to grain size) and the generally loose sexine architecture. Even replacing the 'upsidedown drain and dry phase' of Erdtman (1960 by an evaporation phase in glycerin (Van der Ham, 1990) in order to avoid problems with the penetration of the glycerin jelly (Praglowski, 1970) could not always prevent collapse, which sometimes frustrated the aim of measuring 10 pollen grains per sample. Collapse and invagination of the sulcus margins in monosulcate grains made it very difficult to measure the polar axis (P) and short equatorial axis (E_1), which makes P/E_1 ratios rather meaningless. Therefore measuring was limited to simply recording the length (L = long axis) and the width (S = short axis) of 10 grains (LM). In tetrad configuration (see next section the length represents the long equatorial axis, whereas the width is any of the axes in the plane defined by the polar axis and the short equatorial axis (fig. 1). In a few samples a more reliable appreciation of grain shape could be obtained from critical point dried material.

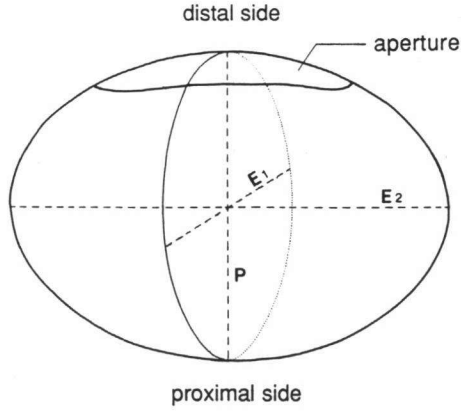

Fig. 1. Schematic lateral view of a monosulcate Stemonaceae pollen grain. P = polar axis, E_1 = short equatorial axis, E_2 = long equatorial axis. The size of any axis in the plane defined by P and E_1 may represent the width (S) of a pollen grain in the present study. The size of E_2 represents the length (L) of the grain.

Measurements relating to pollen wall architecture and stratification were recorded using SEM and TEM images.

STEMONACEAE

Stemonaceae pollen is small to medium-sized [L = 13 (25.0) 40 µm, S = 10 (19.1) 29 µm]. Equatorial outline is elliptical to circular. The grains are monosulcate or inaperturate. Rhomboidal tetrads were observed in immature material of *Stemona australiana* (fig. 2). Mature grains are binucleate (*Croomia pauciflora: Bogner 1861* [plate 4: 1]; *Pentastemona sumatrana: de Wilde & de Wilde-Duyfjes 21399*; *Stemona:* Dahlgren & Clifford, 1982; *Stichoneuron caudatum: Bogner 1789*).

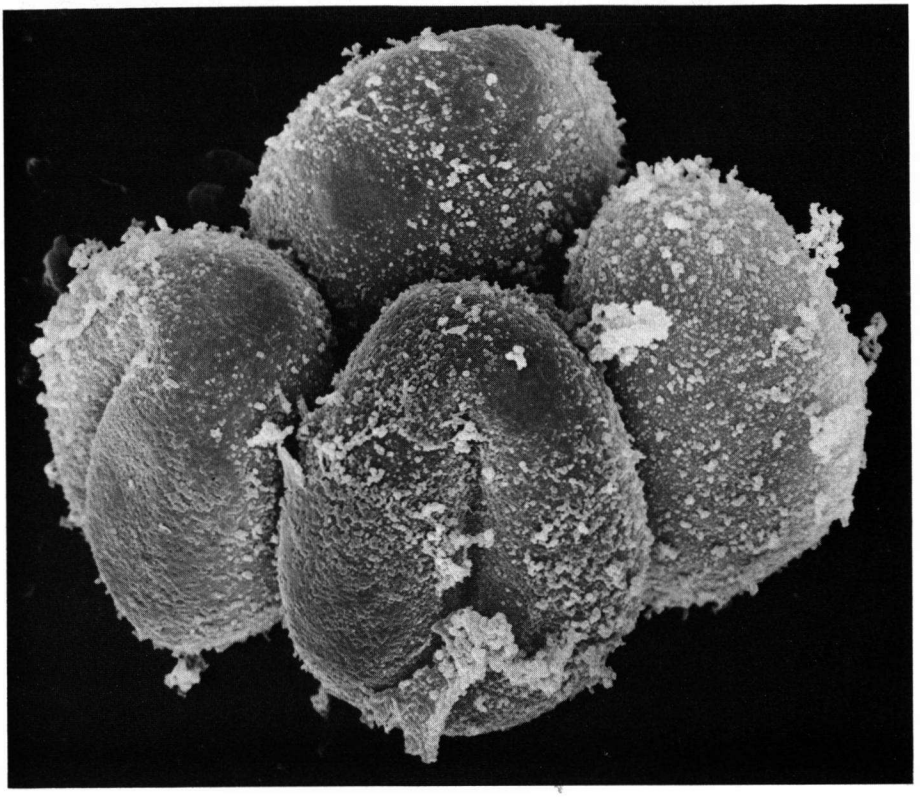

Fig. 2. *Stemona australiana*. Rhomboidal tetrad. Material (immature): *Wightman 1063*, × 2600.

Exine thickness ranges from 0.5 to 1.5 μm at the proximal side (nexine 1/4 to 1/10 of sexine). In monosulcate grains thickness decreases towards the distal side. The infratectal layer is usually columellate, columellate/granular or granular. An infratectal layer is not recognisable in *Pentastemona* pollen, as the entire sexine consists of more or less isodiametric scabrae. The presence of an endexine is questionable. TEM samples from all four genera show contrasting (usually electron-opaque) material at the inner side of the nexine, most distinctly in *Pentastemona* (plate 6). Some lamellation can sometimes be observed (plate 10: 2). Unfortunately, it could not be decided whether the contrasting material is a structurally different acetolysis-resistant sublayer.

Exine ornamentation is (micro)reticulate, rugulate, scabrate, fossulate or psilate, *Stemona* pollen being most diverse. In several *Stemona* species the proximal side shows deviating ornamentation.

Intine morphology is diverse. Generally the apertural intine (oncus) may show three sublayers. The inner one (Kress & Stone, 1982: endintine) is mostly continu-

ous with the nonapertural intine. The middle one (Kress & Stone, 1982: exintine) contains electron-opaque inclusions or tubular/vesicular structures, and is usually the main part of the oncus. The outer sublayer is defined by the absence of distinct inclusions and structures, and is usually thin and largely confined to the oncus.

Pollenkitt/tryphine-like material was observed in pollen of each genus, particularly on the nexine surface and infratectal parts (plates 4: 2; 14: 2).

Ubisch bodies were found on the inner side of the anther wall in all four genera, and sometimes on pollen grains too.

Croomia – Plates 1, 3, 4

Croomia pollen is medium-sized [L = 26 (29.4) 33 µm, S = 18 (21.9) 29 µm]. Equatorial outline is elliptical in acetolysed grains but more circular in critical point dried material. The grains are monosulcate. The sulcus measures c. 4/5 of the grain's long axis.

Exine thickness is c. 1.2 µm at the proximal side (nexine 1/4), and decreases towards the sulcus. Exine stratification is distinct with LM. The infratectal layer is columellate.

Exine ornamentation is reticulate. The lumina are from very small and circular up to 2 µm and irregularly shaped. Lumen size decreases near the sulcus and sometimes near the distal side too (plate 3: 5; see also Ikuse, 1956, pl. 5: 10). The sulcus is irregularly demarcated (plate 3: 5), and is sometimes crossed by several sexine strips (plate 3: 6). The muri are uni- or duplicolumellate and 0.2 to 0.6 µm wide, often with crenulate or sinuous edges. The nexine floor of the lumina shows 0.1 to 0.2 µm large scabrae.

The oncus is c. 15 times as thick as the nonapertural intine. The endintine is indistinct, the oncus being filled with vesicular structures (often with electron-opaque material) throughout.

The anther wall is sparsely covered with smooth Ubisch bodies.

Croomia japonica and *C. pauciflora* have similar pollen. Lumen size is slightly smaller in the latter (compare plate 3: 1 and 5).

Pentastemona – Plates 2, 5, 6

Pentastemona pollen is small-sized [L = 13 (16.1) 23 µm, S = 10 (14.0) 20 µm], and has an elliptical to circular equatorial outline. Although TEM demonstrated the presence of a distinct oncus (plate 6: 1) the exine is inaperturate. Critical point dried grains of *P. egregia* show an elliptical, variably undulate area that might indicate the oncus (plate 5: 1).

Exine thickness is c. 0.6 µm throughout (nexine 1/3 to 1/2). No sexine stratification could be detected (sexine intectate).

Exine ornamentation is scabrate. The scabrae stand on the nexine (plate 5: 4), and are more or less densely arranged, in *P. sumatrana* sometimes in an irregularly microreticulate pattern (plate 5: 7). Individual scabrae are roughly spherical elements of 0.3

to 0.5 μm in diameter. Smaller scabrae are scattered between the larger ones. The larger scabrae have up to 10 smaller scabrae (0.1 to 0.2 μm) on their distal side.

The oncus is c. 7 times as thick as the nonapertural intine. The endintine is indistinct, the oncus being filled with irregularly shaped electron-opaque inclusions throughout. The outer sublayer is rather thick and joins the nonapertural intine.

The anther wall is more or less densely covered with scabrate Ubisch bodies, which are similar to the scabrae of the pollen grains. In acetolysed material (SEM) Ubisch bodies were sometimes observed to be still extensively coherent, forming up to 50 μm large aggregates (plate 5: 5). Still larger structures were found in unacetolysed material (plate 2: 19, 20).

Pentastemona egregia and *P. sumatrana* have similar pollen.

Stemona – Plates 1, 2, 8–12

Stemona pollen is small to medium-sized [L = 19 (28.0) 40 μm, S = 14 (19.6) 29 μm]. Equatorial outline is elliptical in acetolysed grains but more circular in critical point dried material. The grains are monosulcate. The sulcus usually measures 2/3 to 4/5 of the grain's long axis.

Exine thickness is from 0.5 to 1.5 μm at the proximal side (nexine 1/10 to 1/3), and decreases distinctly towards the sulcus (plates 10: 1, 4; 12: 1). Exine stratification is usually indistinct with LM. The infratectal layer is columellate, columellate/granular or granular.

Exine ornamentation is microreticulate, rugulate, scabrate, fossulate or psilate. All types show deterioration along the sulcus, the sexine becoming thin and discontinuous to form a scabrate cover loosening up towards the middle of the aperture membrane.

The oncus is 6 to 12 times as thick as the nonapertural intine. The endintine is indistinct. The oncus shows tubular/vesicular structures that usually contain electron-opaque material.

Smooth Ubisch bodies were sparsely found on the anther wall in *S. wardii* and on pollen grains in *S. parviflora* (plate 9: 1).

Infrageneric variation

Stemona pollen is diverse with respect to exine ornamentation. Five main types and five subtypes characterise single species or groups of species, as shown in Table 1 on the next page.

All types and subtypes are clear-cut with SEM. The types 1a, 1b, 2, 3b and 3c are distinct with LM too (see plates 1, 2). The types 3a, 4 and 5 cannot be distinguished from each other with LM.

The microreticulate type is not homogeneous. Pollen of *S. phyllantha* has lumina and muri of different width (plate 8: 3), whereas pollen of *S. kerrii* has a much more regular reticulum of narrow muri (plate 8: 5). See also next section.

The muri in the rugulate type are sometimes arranged in a vaguely reticulate pattern (*S. tuberosa: Bogner s.n.*).

Table 1. Infrageneric variation of a number of pollen features in *Stemona*.

ornamentation	species	exine thickness	average L
1. microreticulate			
a. irregular form (8: 3):	*phyllantha*	1–1.5	35.6
b. regular form (8: 5):	*kerrii*	1	21.7
2. rugulate (11: 2):	*javanica*	1–1.5	27.0
	tuberosa	1–1.5	29.3
3. scabrate			
a. all over (9: 2):	*parviflora*	0.5	28.3
b. prox. rugulate (9: 6):	*lucida*	1.5	26.7
c. prox. psilate (9: 4):	*japonica*	1–1.5	31.0
	sessilifolia	1–1.5	29.1
4. fossulate (11: 4):	*cochinchinensis*	0.5–1	25.4
	collinsae	0.5	26.5
	curtisii	0.5–1	27.8
5. psilate (11: 6):	*australiana*	0.5	31.2
	prostrata	0.5	20.4
	wardii	0.5	32.3

Pollen of the scabrate type is scabrate all over (*S. parviflora*, plate 9: 1), or it shows deviating ornamentation on the proximal side, either as up to 3 μm large rugulate muri (*S. lucida*, plate 9: 5) or as more or less extensive (im)perforate psilate areas (*S. japonica, S. sessilifolia*). Pollen of *S. japonica* shows two perforate areas that join in the middle of the proximal side, and change circumferentially into the surrounding scabrae (plate 9: 3). In *S. sessilifolia* the psilate areas are imperforate, smaller and more numerous.

Exine thickness is 1 to 1.5 μm in the types 1, 2, 3b and 3c, and 0.5 to 1 μm in the types 3a, 4 and 5.

Grain size shows long ranges in the microreticulate type and psilate type. *Stemona kerrii* and *S. prostrata* have small-sized pollen, whereas *S. phyllantha, S. australiana* and *S. wardii* have relatively large pollen.

Stemona pollen also varies as to the structure of the infratectal layer. One extreme is represented in *S. phyllantha*, where the infratectum is columellate (plate 8: 4). The other is shown by *S. japonica*, where the entire, rather thick infratectal layer is finely granular almost throughout the grain (plate 10: 1–3). It was designated by Zavada (1983) as the *Stemona*-type of monocot pollen. Locally, short columellae may be inserted, especially at the proximal and distal side.

In columellate/granular infratectums the granules are distributed immediately below the tectum (plates 8: 6; 10: 5; 12: 3, 4). Such a distribution was also recorded in unrelated plants such as *Artemisia* (Compositae; Bhandari, 1984), *Bauhinia* (Leguminosae; Ferguson & Pearce, 1986: fig. 42, 45) and *Dodonaea* (Sapindaceae; Muller & Schuller, 1989: fig. 120/II/3). A columellate/granular infratectum occurs in *S. australiana, S. cochinchinensis, S. curtisii, S. kerrii, S. lucida, S. prostrata* and *S. tuberosa*. Infratectal structure is still unknown in *S collinsae, S. javanica, S. sessilifolia* and *S. wardii*.

In *S. phyllantha* the lumina of the microreticulate tectum show a more or less depressed fine reticulum (plate 8: 3). Such a reticulum (though less continuous, and obscured by adhering and merging granules) is also found in the lumina of the microreticulate pollen of *S. kerrii* (*BKF 32037*, plate 8: 5). These depressed fine reticulums are considered to form part of the infratectum too.

Stichoneuron – Plates 1, 13, 14

Stichoneuron pollen is small to medium-sized [L = 20 (26.6) 35 µm, S = 15 (21.1) 28 µm]. Equatorial outline is elliptical in acetolysed grains but about circular in critical point dried material. Most grains show an elongate aperture. However, the variable length of this aperture (from zero up to as long as the grain's long axis) and the clear exine stratification along its edge strongly suggest that the exine is inaperturate, the aperture being actually a crack..

Exine thickness is c. 1.2 µm throughout (nexine 1/4). Exine stratification is distinct with LM. The infratectal layer is columellate.

Exine ornamentation is microreticulate. The lumina are more or less isodiametric, and from very small up to 1.2 µm. Lumen size does not decrease towards the aperture. The muri are unicolumellate, and 0.2 to 0.6 µm wide.

The oncus is 3 to 4 times as thick as the nonapertural intine. The endintine is distinct. The exintine shows tubular/vesicular structures that often contain electron-opaque material.

The anther wall is sparsely covered with smooth Ubisch bodies.

Stichoneuron caudatum and *S. membranaceum* have similar pollen.

POLLEN AND TAXONOMY

The individual genera of the Stemonaceae are pollen-morphologically more or less homogeneous, and represent natural entities.

Stemona pollen is rather diverse as to ornamentation but it is clearly held together by the structure of the infratectal layer. The presence of infratectal granules and/or reticulums is considered an apomorphy of *Stemona* pollen. Within *Stemona* fine reticulums are possibly plesiomorphic (*S. phyllantha*), and granules apomorphic (*Stemona* spp.). Intermediate states occur in *S. kerrii*. Loss of columellae (infratectum granular), as in pollen of *S. japonica*, is generally considered as apomorphic in monocotyledons (see also Walker, 1976 and Zavada, 1983).

Table 2. Features of Stemonaceae pollen.

	Croomia	*Stemona*	*Stichoneuron*	*Pentastemona*
grain size (µm)	26 (29.4) 33	19 (28.0) 40	20 (26.6) 35	13 (16.1) 23
apertural system sexine	monosulcate tectate	monosulcate tectate	inaperturate tectate	inaperturate intectate
infratectal layer	columellate	(columellate) columellate/granular (granular)	columellate	—
ornamentation	reticulate	microreticulate rugulate scabrate fossulate psilate	microreticulate	scabrate (= sexine!)
Ubisch bodies	smooth	smooth	smooth	scabrate
oncus	thick	thick	thin	thick
endintine	indistinct	indistinct	distinct	indistinct

The types based on exine ornamentation in *Stemona* pollen reflect macromorphological relationships rather well. B.E.E. de Wilde-Duyfjes (written comm.) lists the following informal groups (the non-Malesian *S. japonica, sessilifolia* and *wardii* not included): *S. australiana* and *S. prostrata* (thin psilate exine), *S. cochinchinensis, S. collinsae* and *S. curtisii* (fossulate rather thin exine), and *S. javanica, S. lucida* and *S. tuberosa* (thick completely or partly rugulate exine). *Stemona parviflora* and *S. phyllantha* are both related to the *tuberosa* group. The former shares scabrate ornamentation with *S. lucida* of this group. However, pollen of *S. phyllantha* is quite different. *Stemona kerrii* is macromorphologically most distinct. Its pollen is distinct too, being regularly microreticulate, but it shares the presence of infratectal fine reticulums with *S. phyllantha.*

The Stemonaceae as a family is a quite heterogeneous assemblage (table 2). Some resemblances do exist, for example the monosulcate apertural system in *Croomia* and *Stemona,* the tectate/columellate sexine in *Croomia, Stemona phyllantha* and *Stichoneuron,* and the (micro)reticulate ornamentation in *Croomia, Stemona kerrii* and *S. phyllantha,* and *Stichoneuron.* However, these resemblances do not convincingly demonstrate close affinity, as they are probably plesiomorphic character states in the monocotyledons (Walker & Doyle, 1975; Zavada, 1983). The inaperturate exines of *Pentastemona* and *Stichoneuron* must be considered as apomorphic (see also Zavada, 1983). *Stichoneuron* pollen seems to be nearer to the plesiomorphic monosulcate condition than *Pentastemona* pollen. In contrast with the latter it breaks up easily in a monosulcate way, which is possibly due to its heavily channeled exintine. *Croomia* pollen is considered as most plesiomorphic in the Stemonaceae. In *Stemona* much of the plesiomorphic monosulcate/reticulate/columellate state of monocot pollen occurs in *S. phyllantha* and *S. kerrii.*

The morphology of the intine varies from genus to genus. Two types can be distinguished. The oncus is relatively thin and has a distinctly delimited endintine in *Stichoneuron*. It is thick and has an indistinct endintine in *Croomia, Stemona* and *Pentastemona*. Both types were recorded in monocotyledons (Kress & Stone, 1982). However, little is known of oncus types in this large group, and still less of their evolutionary status, which hampers assessing natural affinities.

Pentastemona

The pollen types of *Croomia, Stemona* and *Stichoneuron* can be more or less easily derived from each other (which does not imply affinity!) but that of *Pentastemona* is isolated from the other Stemonaceae pollen. Its inaperturate apertural system is different from that of *Stichoneuron* (see above). Its sexine architecture is most deviating. The sexine consists entirely of scabrae that seem randomly organised and do not show differentiation into tectal and infratectal parts (sexine intectate). A striking feature is the resemblance between these scabrae and the Ubisch bodies on the anther wall (plate 5: 5). Other Stemonaceae show smooth Ubisch bodies that bear no special resemblance with sexine elements.

Sexine versus Ubisch bodies

Ubisch bodies, also called (tapetal) orbicules, are sporopolleninous bodies of unknown function that originate along the radial and inner tangential walls of tapetum cells during the free-grain period of microsporogenesis (Bhandari, 1984; Pacini, 1990). They are common in seed plants with a secretory tapetum, and are found on tapetum remains and pollen grains towards anther dehiscence, either as globoid up to 0.8 μm large isolated bodies or as larger, usually flattened structures. They may also be connected and incorporated to form part of an acetolysis-resistant tapetal membrane (see for reviews: Bhandari, 1984 and Shivanna & Johri, 1985). This apparently occurs in *Pentastemona egregia*. Besides being present as a loose cover Ubisch bodies locally form dense aggregates, large fragments of which were observed in acetolysed material (plate 5: 5). Their size ranges from 0.1 to 0.5 μm, and like the scabrae on the pollen grains the larger ones may show a scabrate surface. They lack an electron-lucent centre (pro-Ubisch body). A fragmentary peritapetal membrane (see Bhandari, 1984) is possibly also present (plate 6).

Scabrate Ubisch bodies are not rare among seed plants. They are found, for example, in Gramineae (Banerjee, 1967: fig. 6; Christensen et al., 1972), Liliaceae (Reznickova et al., 1980: figs. 10–12), Trilliaceae (Takahashi, 1982: fig. 5), Sapindaceae (Muller & Schuller, 1989: fig. 120/II/3) and Cupressaceae (Bortenschlager, 1990: e.g. fig. 6D). Probably homologous bodies were found in several ferns (Lugardon, 1981). Similar though not acetolysis-resistant structures occur in the moss *Andreaea rothii* on developing spores (perine) and in mature capsules on the cells lining the spore sac (Brown & Lemmon, 1990: figs. 8a, 14b–d).

Neither is the resemblance between ornamentation of pollen and spores and that of Ubisch bodies to be regarded as a rare phenomenon. It was reported in ferns (Lugardon, 1981), grasses (Banerjee, 1967) and several other, unrelated families

(see Raj & El-Ghazaly, 1987). It could even be noticed in fossil material (Taylor, 1990). In all these cases, however, the similarity concerns only the sculptural aspect, the structure of the sexine and Ubisch bodies being essentially different.

Overall resemblance, including the structural aspect, is known only in *Pentastemona* (present study) and *Trillium* (Trilliaceae; Takahashi, 1982). In both genera the sexine consists of randomly arranged Ubisch body-like elements, though a more or less tectate/columellate sexine and other sexine types occur in *Trillium* as well. A further correspondence is their inaperturate exine, ornamentation being homogeneous throughout the pollen grain. It would appear that the amount of genetic information needed in patterning the whole sexine in these taxa is little or no more than that used by tapetum cells to develop Ubisch bodies.

Christensen et al. (1972) and Reznickova & Willemse (1980) stressed the broad resemblance between sexine formation and Ubisch body development in *Sorghum* and *Lilium* respectively. Considering this it is not hard to imagine that in absence of additional information for patterning, vertical (tectate/columellate structure) as well as horizontal (any elaborate form of ornamentation), a microspore may develop a cover of randomly arranged Ubisch body-like sexine elements. The ontogeny of such a sexine and the Ubisch bodies may include simple condensation and aggregation processes, in which purely physical spacing effects may be involved in patterning (Blackmore & Barnes, 1990; Van Uffelen, 1991).

Phylogenetically the presence of a secretory tapetum is a plesiomorphy of all land plants, and the production of acetolysis-resistant bodies is probably plesiomorphic in tracheophytes (Lugardon, 1981; Pacini et al., 1985; Pacini, 1990). A tectate/columellate monosulcate exine is a plesiomorphic feature of monocot pollen. The scabrate sexines of *Pentastemona* and *Trillium* may be considered as apomorphic. They would represent reduced states as to patterning and apertural system: loss of vertical patterning (sexine consisting of scabrae without differentiation into tectum and columellate layer), loss of horizontal patterning (sexine elements random, no differentiation into apertural and nonapertural areas), and loss of the sulcus (no differentiation into apertural and nonapertural nexine). Sexine formation appears to be reduced to developing Ubisch body-like scabrae in an Ubisch body-like arrangement through possibly very basic processes.

Affinities of Stemonaceae

Followjng the system of Dahlgren et al. (1985) the Stemonaceae, together with the Trilliaceae, Dioscoreaceae, Trichopodaceae, Taccaceae, Smilacaceae and Petermanniaceae make up the order Dioscoreales. The two latter families form a bridge between the Dioscoreales and Asparagales. The Stemonaceae and Trilliaceae approach the Dioscoreaceae and Trichopodaceae, though *Scoliopus* of the Trilliaceae has affinity with the Liliaceae s.s. The Trichopodaceae would be a link between the Taccaceae and the rest of the Dioscoreales. Thus, according to Dahlgren et al. (l.c.) the Trilliaceae, Dioscoreaceae and Trichopodaceae are possibly the closest relatives of the Stemonaceae. Judging from Van Steenis' description Dahlgren et al. found the genus *Pentastemona* highly distinctive, about as distinct as *Trichopus* and *Tacca*, and thus worthy of family rank.

Huber (1991) holds a rather different opinion. The Dioscoreales should embrace only the Dioscoreaceae, Stenomeridaceae (as *Stenomeris* in the Dioscoreaceae in Dahlgren's system) and Trichopodaceae. The Stemonaceae (as Roxburghiaceae), Trilliaceae and Smilacaceae were transferred to the Asparagales, and the Taccaceae to the Philydrales. *Pentastemona* would be related to the Araceae (*Pentastemona* was originally described as an araceous genus) and Scitamineae (= Zingiberales) rather than to the Stemonaceae.

It is very difficult to make meaningful comparisons between pollen of Stemonaceae and that of supposedly related taxa, as detailed monographic pollen studies are very scarce. Without further knowledge (SEM and TEM) it is hardly possible to evaluate the relationships of the Stemonaceae. Features like monosulcate exine, columellate infratectum and (micro)reticulate ornamentation are plesiomorphic states of monocot pollen, which may occur in not closely related groups. An inaperturate exine like that of *Pentastemona* and *Stichoneuron* pollen is a common homoplasy in monocotyledons (Dahlgren & Clifford, 1982). Remarkably, however, it is found in all Zingiberales, many Araceae, nearly all Smilacaceae, and in *Trillium* of the Trilliaceae. The granular infratectum of *Stemona* is known in the taxa mentioned above only in advanced Araceae (Grayum, 1986). A scabrate sexine architecture like that of *Pentastemona* pollen occurs in *Trillium* (see previous section) as well as in several Zingiberales (Dahlgren & Clifford, 1982). Pollen of these taxa differ from *Pentastemona* pollen in having a very thin nexine or no nexine at all. Scabrate sexine architecture does probably not occur in Araceae pollen.

Another pollen-morphological link between *Pentastemona* and Asparagales (if one accepts Huber's view on the position of *Trillium*)) is *Peliosanthes* of the Convallariaceae. This genus, monotypic according to Jessop (1976) but including rather different flower and pollen morphologies, belongs to the tribe Ophiopogoneae, which is possibly not closely related to the rest of the family (Stützel et al., 1991). Its floral morphology reminds of that of *Pentastemona*. Compare Dahlgren & Clifford (1982: 41 I) and Dahlgren et al. (1985: 55 O–Q, 56 F, G) with Van Heel (1992, in prep.); figures16e–g in Jessop (1979) represent an *Ophiopogon* species rather than a *Peliosanthes*. *Peliosanthes* pollen shows a variously scabrate (plate 7: 2–4) to vaguely tectate/columellate (plate 7: 5, 7) sexine that resembles the cover of Ubisch bodies on the anther wall sometimes very much (plate 7: 1, 2). However, the exine is monosulcate (though not very clearly). The nexine is as thick as in *Pentastemona* but differs in being rather irregular and crumbly (plate 7: 6, 7). The Ubisch bodies are not solid but possess an electron-lucent centre (pro-Ubisch body, plate 7: 7). Intine morphology is also rather different, channels or vesicles being present in the exintine throughout the pollen grain (plate 7: 7).

A scabrate (Ubisch body-like) sexine structure and an inaperturate exine should be considered as apomorphic features. The main question is, of course, whether these derived states are autapomorphic (homoplasies) or synapomorphic (homologues). Pollen of *Pentastemona, Trillium* and *Peliosanthes* may be strikingly similar (compare for instance plates 5: 3 and 7: 3), but one must bear in mind that apomorphies such as scabrate sexine structure and inaperturate exine may represent reduced states. Sexine formation is possibly controlled then by basic processes in which physical factors play an important role. This might easily lead to close but in phylogenetical

sense superficial resemblance (homoplasy). Disappearance of the sulcus might be correlated with reduced patterning. Aperture membranes often show a scabrate, Ubisch body-like cover (see for instance Cronk & Clarke, 1981: figs. 1, 2). If the nonapertural sexine is reduced to scabrae (as in *Peliosanthes*), it is only a small step further towards the inaperturate exine of *Pentastemona* and *Trillium*. Evidently the question whether the similarities are homologues or homoplasies is hard to answer without further evidence. A cladistic analysis of the Stemonaceae and supposedly related groups, including data from as many disciplines as possible, might eventually provide a hypothesis concerning the relationships.

CONCLUSION

The Stemonaceae appear to be a eurypalynous family. The genera represent natural entities but the intergeneric bonds are rather weak. Similarities between genera (e.g. columellate infratectum, (micro)reticulate ornamentation, monosulcate exine) are probably monocot plesiomorphies, which are unreliable indicators of close affinity, whereas the apomorphies are limited to single genera (infratectal granules and reticulums in *Stemona*, sexine consisting of Ubisch body-like elements in *Pentastemona*). The inaperturate apertural systems of *Pentastemona* and *Stichoneuron* pollen are probably not homologous. *Croomia* pollen is considered to have most plesiomorphies, whereas *Pentastemona* pollen is regarded as most apomorphic.

Pentastemona pollen is most deviating in the Stemonaceae. This would support family rank. The important question whether the Stemonaceae s.s. are the closest relatives of *Pentastemona*, cannot be answered at present. Features that separate *Pentastemona* from other Stemonaceae (inaperturate exine, scabrate sexine architecture) are more or less common in Asparagales and Zingiberales. However, further evidence is needed to decide upon homology or homoplasy of these similarities.

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EXPLANATION OF PLATES

Plate 1. Stemonaceae, LM. From left to right: proximal side, optical section, and distal side with aperture; × 1000.
— 1–3: *Croomia japonica* (sheet 908.225-1376).
— 4–6: *Stichoneuron caudatum* (*Stone & Sidek 12514*).
— 7–9: *Stemona phyllantha.*
— 10–12: *Stemona kerrii* (*Santisuk & Warncke 2351*).
— 13–15: *Stemona tuberosa* (*Treub 1893*).
— 16–18: *Stemona lucida.*

Plate 2. Stemonaceae, LM. From left to right: proximal side, optical section, and distal side (except for *Stemona curtisii* and *Pentastemona egregia*); × 1000. 4, 8, 12, 16, 18 and 19 with 'interference contrast' (IC).
— 1–3: *Stemona japonica* (*d'Alleizette 7353*).
— 4–7: *Stemona parviflora.*
— 8–11: *Stemona cochinchinensis* (*Kerr 21335*).
— 12–15: *Stemona prostrata.*
— 16, 17: *Stemona curtisii:* proximal side, with and without IC.
—18–20: *Pentastemona egregia* (*Bogner 1724*, unacetolysed pollen in chlorallactophenol) – 18: ornamentation (proximal and distal side not distinguishable); 19, 20 (with and without IC): optical sections and membranes with Ubisch bodies (arrows).

Plate 3. *Croomia*, SEM.
— 1, 2, 4: *C. japonica* (sheet 908.225-1377). 1: proximal view, × 2000; 2: detail proximal side showing reticulate ornamentation, × 8000; 4: section proximal side, × 7000.
— 3, 5, 6: *C. pauciflora* – 3: distal view, × 1600; 5: lateral view of collapsed grain showing proximal side (top) and sulcus margin (bottom), × 1350; 6: detail of distal side showing middle part of sulcus with crossing sexine strips, × 8000.

Plate 4. *Croomia*, TEM.
— 1–3: *C. pauciflora* – 1: cross section showing exine and intine stratification, × 4800; 2: detail of proximal side, × 14400; 3: detail of distal side with oncus, × 8400.

Plate 5. *Pentastemona*, SEM.
— 1–5: *P. egregia* (1: *Bogner 1724*, CPD; 2–5: *Meijer 17010*) – 1: two inaperturate grains showing undulate areas possibly indicating onci, × 1750; 2: collapsed inaperturate grain, × 3250; 3: detail scabrate ornamentation, × 8000; 4: detail of scabrae in distal and lateral view showing sexine architecture, × 16500; 5: part of pollen grain (bottom) and aggregated Ubisch bodies (top), × 5500.

(Plate 5. *Pentastemona*, SEM).

— 6, 7: *P. sumatrana* (*de Wilde & de Wilde-Duyfjes 21399*, CPD) – 6: inaperturate grain, × 8000; 7: detail scabrate ornamentation, × 14500.

Plate 6. *Pentastemona*, TEM.

— 1, 2: *P. egregia* (*Bogner 1724*) – 1: section showing exine and intine stratification, anther wall with Ubisch bodies, fragmentary peritapetal membrane(?), and endothecial cell wall thickening (arrow), × 6900; 2: detail of 1 showing part of oncus, × 23200.

Plate 7. *Peliosanthes* Andr. (Convallariaceae), SEM and TEM.

— 1–7: *P. teta* Andr. (1, 2: *Kerr 17977*, Thailand, CPD; 3: *Kramer & Nair 6223*, India; 4: *Geesink & Hiepko 7903*, Thailand; 5: *Beusekom et al. 828*, Thailand; 6: *Holstvoogd 737*, Java; 7: *d'Alleizette 7210*, India; 1–4, 6: subsp. *humilis* (Andr.) Jessop, 5, 7: subsp. *teta*) – 1: monosulcate grain against anther wall with Ubisch bodies, × 1950; 2: detail of 1, × 5000; 3–5: details of scabrate to fossulate ornamentation, × 8000; 6: exine and intine stratification, × 20300; 7: exine and intine stratification, and Ubisch bodies, × 18700.

Plate 8. *Stemona*, SEM.

— 1–4: *S. phyllantha* – 1: proximal view, × 1400; 2: distal side, × 1550; 3: detail of 1 showing irrgularly microreticulate ornamentation, × 8000; 4: detail of 2 showing exine stratification, × 8000.

— 5, 6: *S. kerrii* (5: *BKF 32037*, CPD; 6: *Larsen et al. 2351*) – 5: detail of regularly microreticulate ornamentation, × 8000; 6: wall sections showing exine architecture, × 8000.

Plate 9. *Stemona*, SEM.

— 1, 2: *S. parviflora* – 1: proximal view, × 1600; 2: detail of 1 showing scabrate ornamentation, × 8000.

— 3, 4: *S. japonica* (*Makino 71842*) – 3: proximal view, × 1600; 4: detail proximal side showing psilate/scabrate ornamentation, × 8000.

— 5, 6: *S. lucida* – 5: proximal view, × 8000; 6: detail proximal side showing rugulate/scabrate ornamentation, × 8000.

Plate 10. *Stemona*, TEM.

— 1–3: *S. japonica* (*d'Alleizette 7353*) – 1: cross section showing proximal side (top) and sulcus (bottom), × 4200; 2, 3: details of 1 showing exine stratification, × 23700.

— 4, 5: *S. lucida* – 4: cross section showing proximal side (on the left) and sulcus (on the right), × 3500; 5: detail of 4 showing exine stratification, × 23700.

Plate 11. *Stemona*, SEM.

— 1, 2: *S. tuberosa* (1: var. *tuberosa*, CPD; 2: var. *ternatensis*, *Robinson 295*) – 1: lateral view (sulcus at top), × 1900; 2: detail proximal side showing rugulate ornamentation, × 8500.

— 3, 4: *S. cochinchinensis* (*Kerr 21335*) – 3: detail distal side showing sulcus margin and aperture membrane, × 8500; 4: detail proximal side showing fossulate ornamentation, × 8500.

— 5, 6: *S. wardii* (CPD) – 5: oblique view showing sulcus with aperture membrane, × 1800; 6: detail proximal side showing psilate ornamentation with perforations, × 8500.

Plate 12. *Stemona*, TEM.

— 1–3: *S. curtisii* – 1: cross section showing exine and intine stratification, × 5200; 2: detail of 1 showing oncus and aperture membrane, × 23500; 3: detail of 1 showing distal exine (top) and proximal exine (bottom), × 25500.

— 4: *S. australiana* (*Versteeg 1913*): proximal (top) and distal (bottom) exine, × 32900

Plate 13. *Stichoneuron*, SEM.

— 1–6: *S. caudatum* (*Bogner 1789*, all except 4 CPD) – 1: inaperturate grain, × 1550; 2: detail of 1 showing microreticulate ornamentation, × 8000; 3: grain with large crack showing intine, × 1700; 4: sections showing exine stratification, × 8000; 5: grain with small crack × 1700; 6: detail of 5, × 5000.

Plate 14. *Stichoneuron*, TEM.

— 1, 2: *S. caudatum* (*Bogner 1789*) – 1: cross section showing exine and intine stratification (oncus at upper right corner), × 4100; 2: detail showing oncus stratification and small crack in exine, × 25000.

Explanation of abbreviations

am = aperture membrane, **c** = columellate infratectal layer, **c/g** = columellate/granular infratectal layer, **CPD** = critical point dried material, **en** = endintine, **end** = endexine, **ex** = exintine, **g** = granular infratectal layer, **ge** = nucleus of generative cell, **i** = intine, **l** = lamellation, **n** = nexine, **o** = oncus, **p** = pollenkitt/tryphine, **pm** = peritapetal membrane, **s** = sexine, **t** = tectum, **u** = Ubisch body, **ve** = nucleus of vegetative cell.

(for plates 1–14, see pages 146–159)

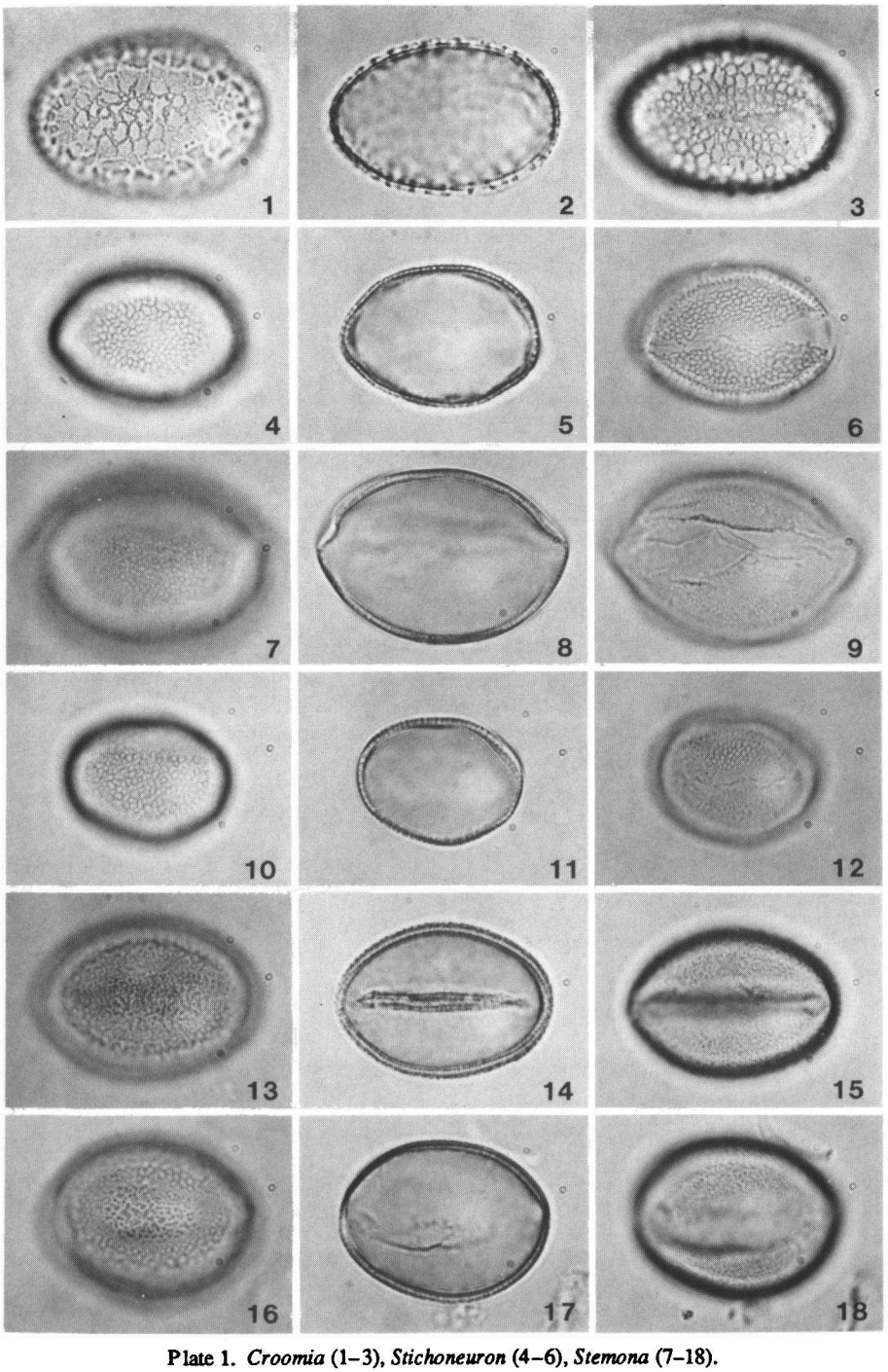


Plate 1. *Croomia* (1–3), *Stichoneuron* (4–6), *Stemona* (7–18).

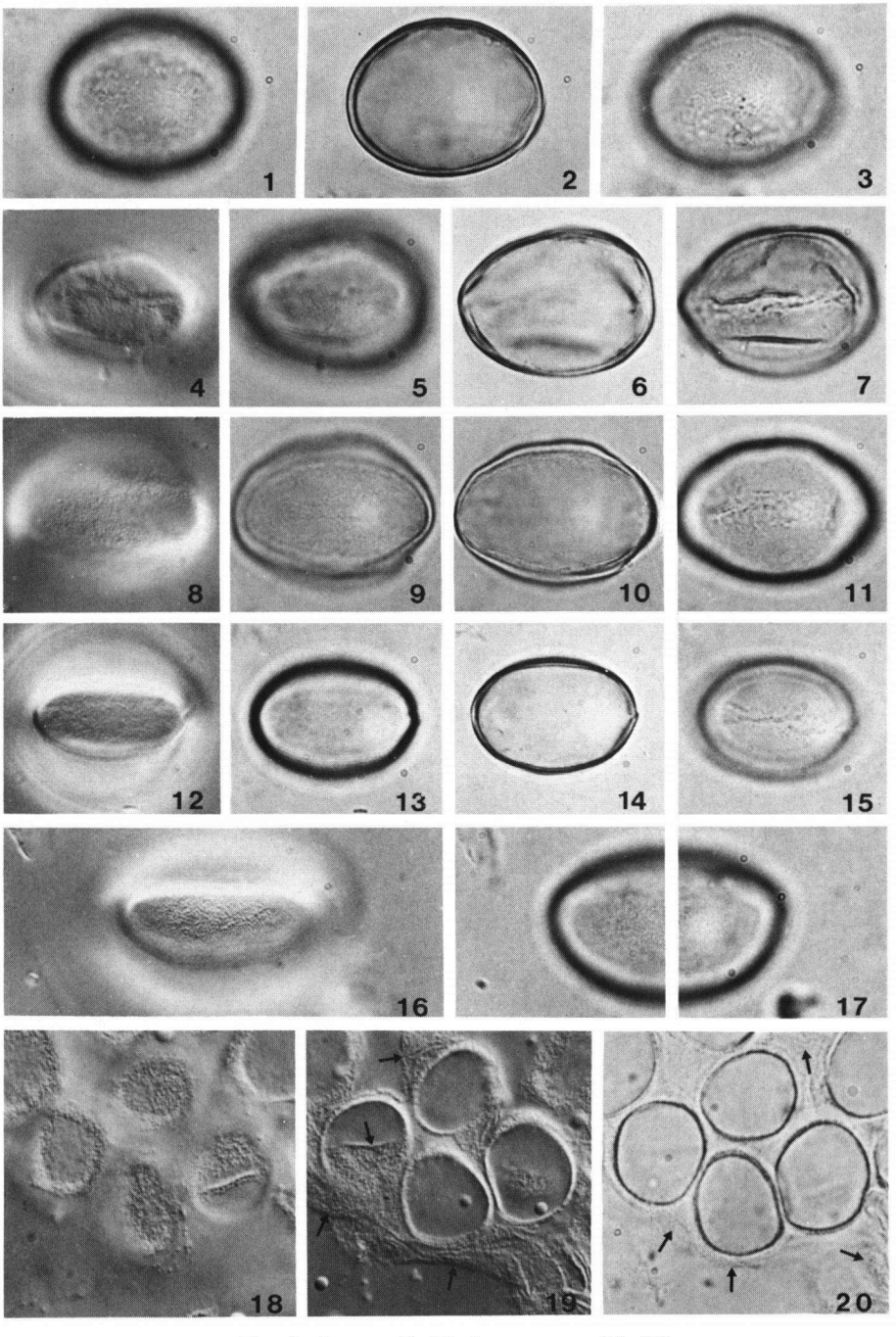


Plate 2. *Stemona* (1–17), *Pentastemona* (18–20).

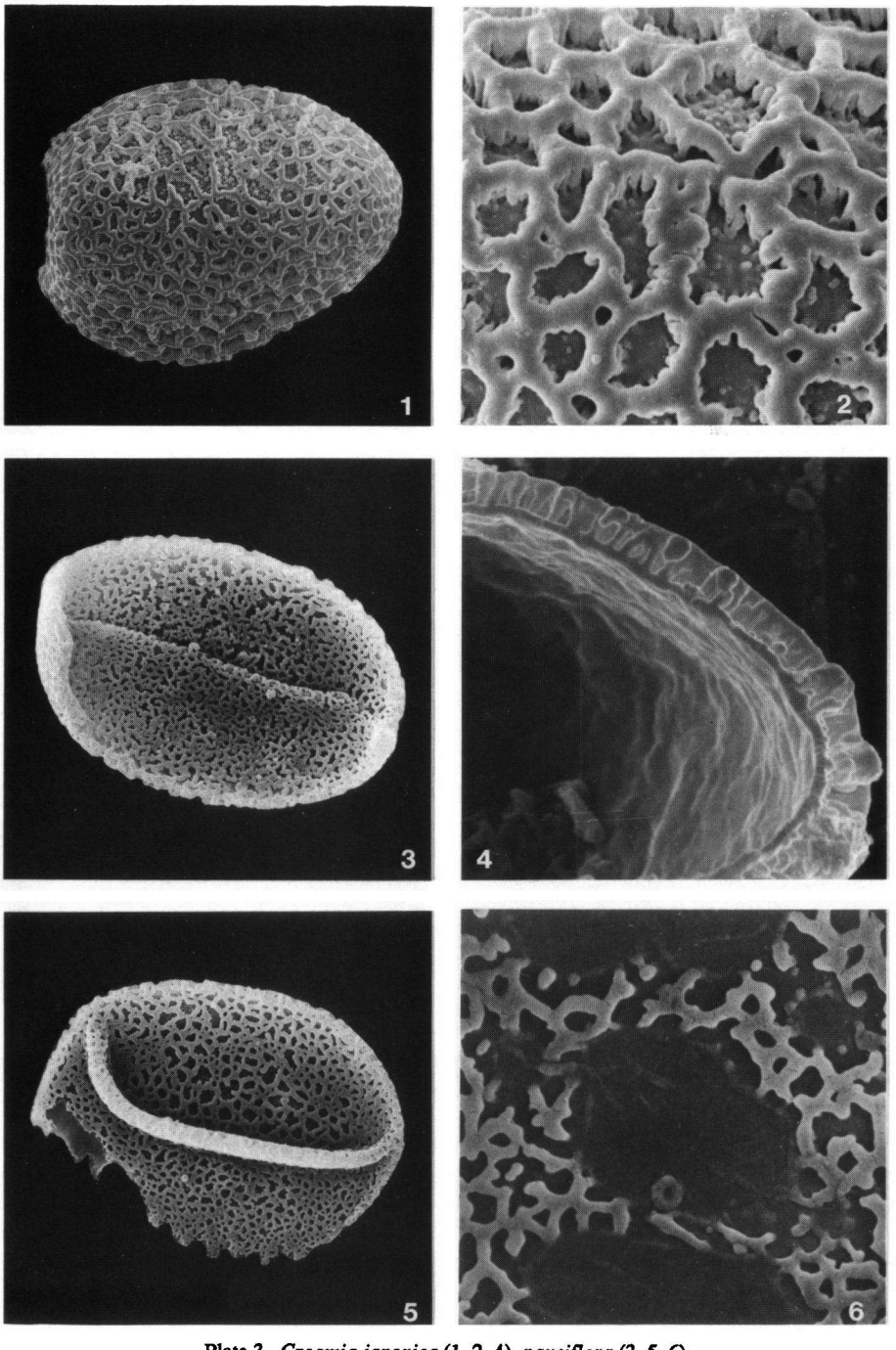


Plate 3. *Croomia japonica* (1, 2, 4), *pauciflora* (3, 5, 6).

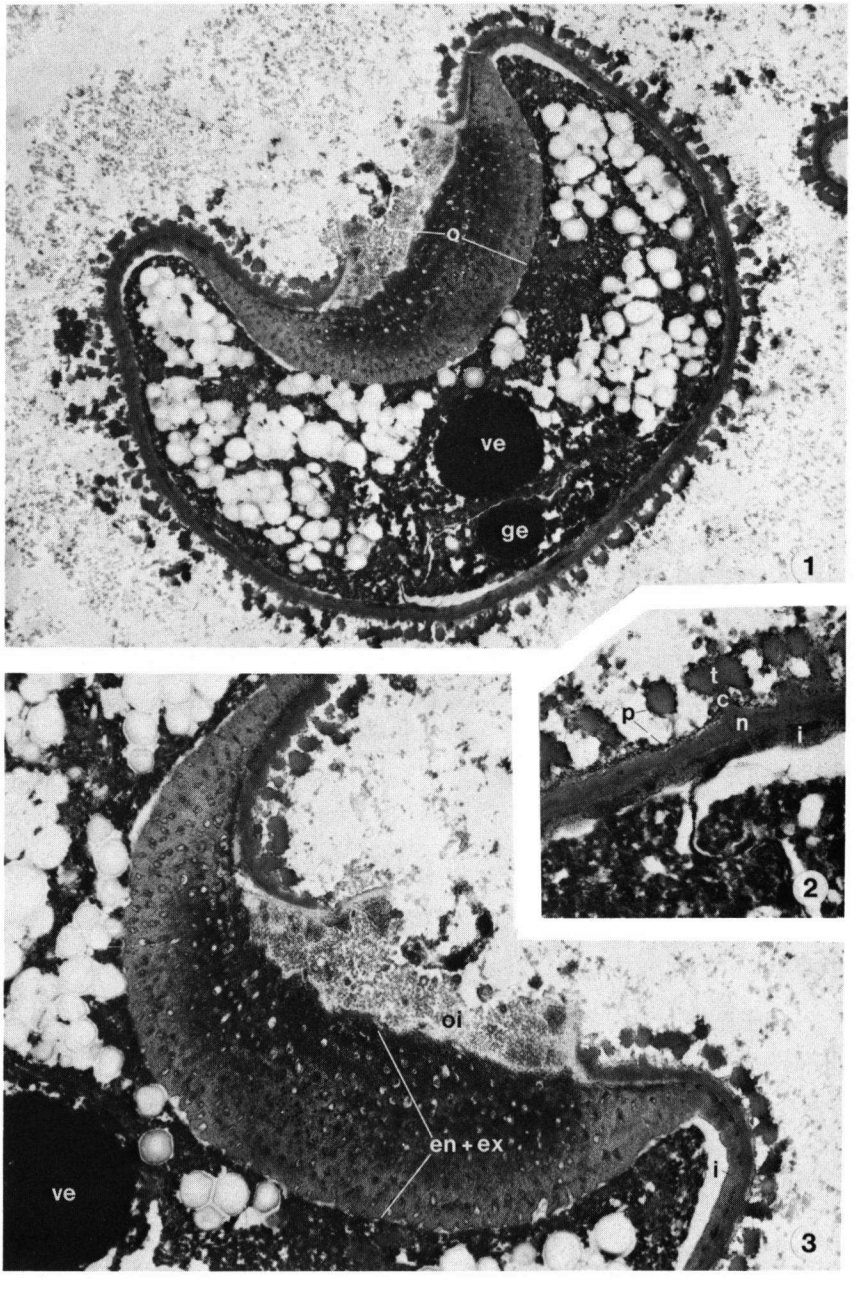


Plate 4. *Croomia pauciflora.*

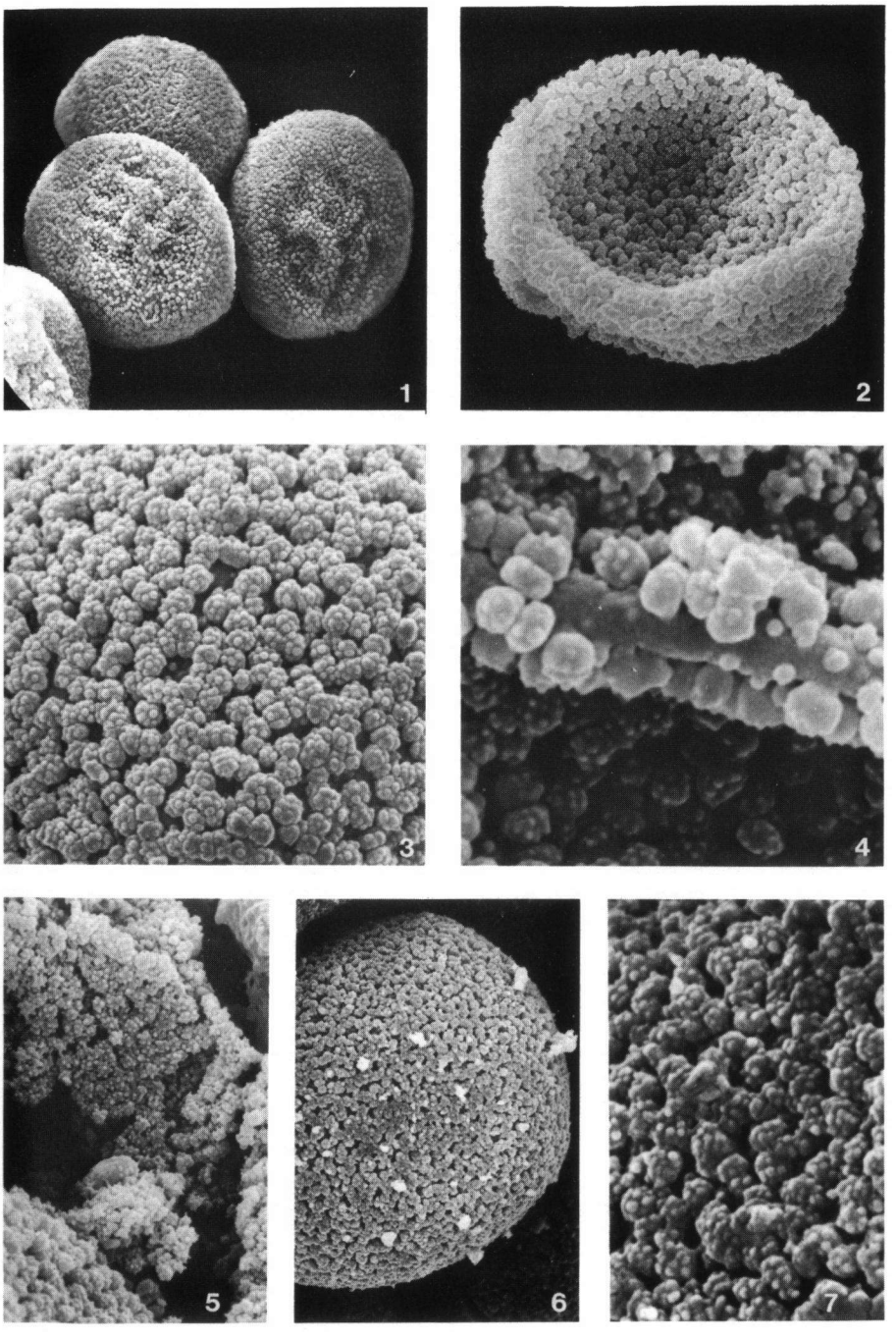


Plate 5. *Pentastemona egregia* (1–5), *sumatrana* (6, 7).

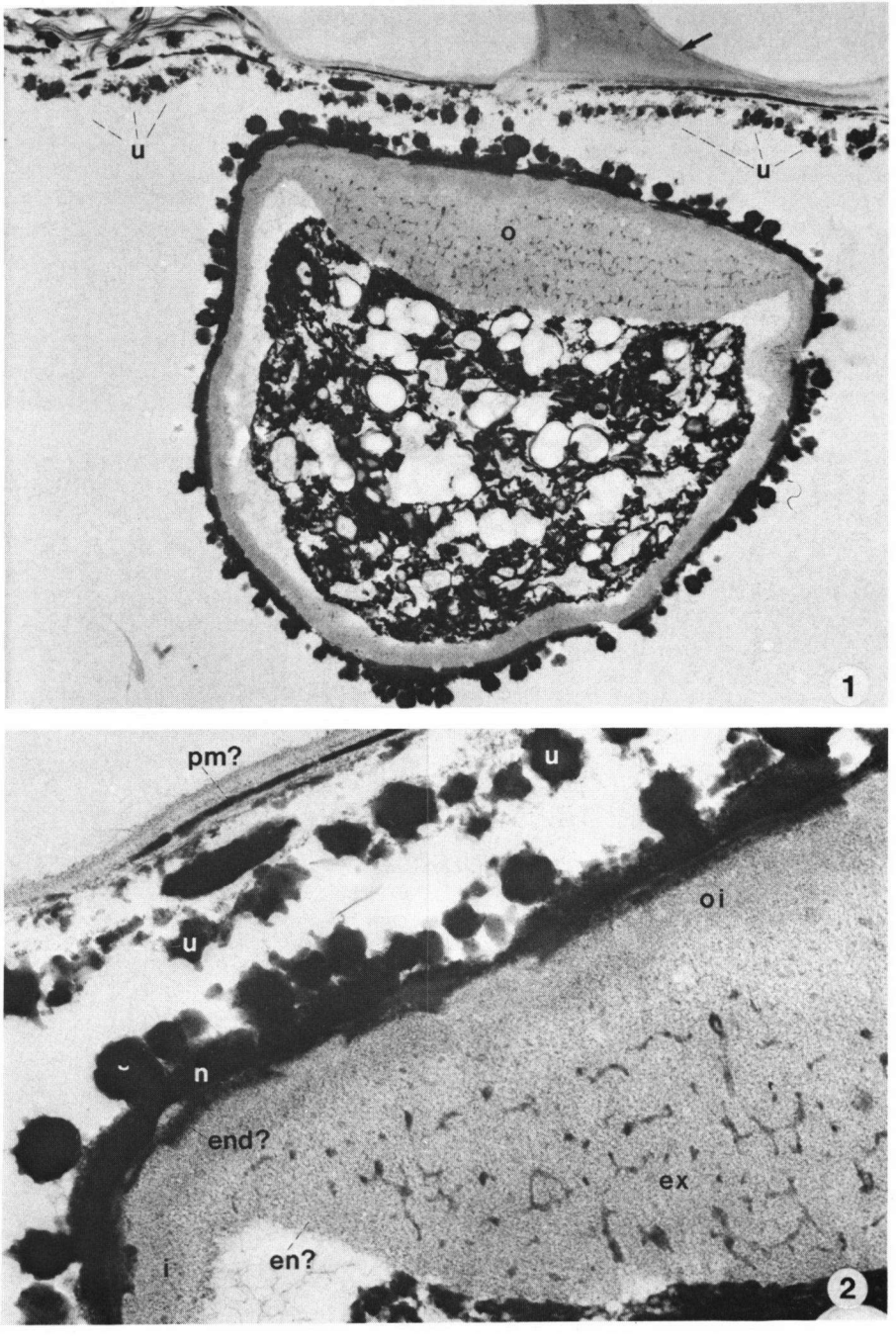


Plate 6. *Pentastemona egregia.*

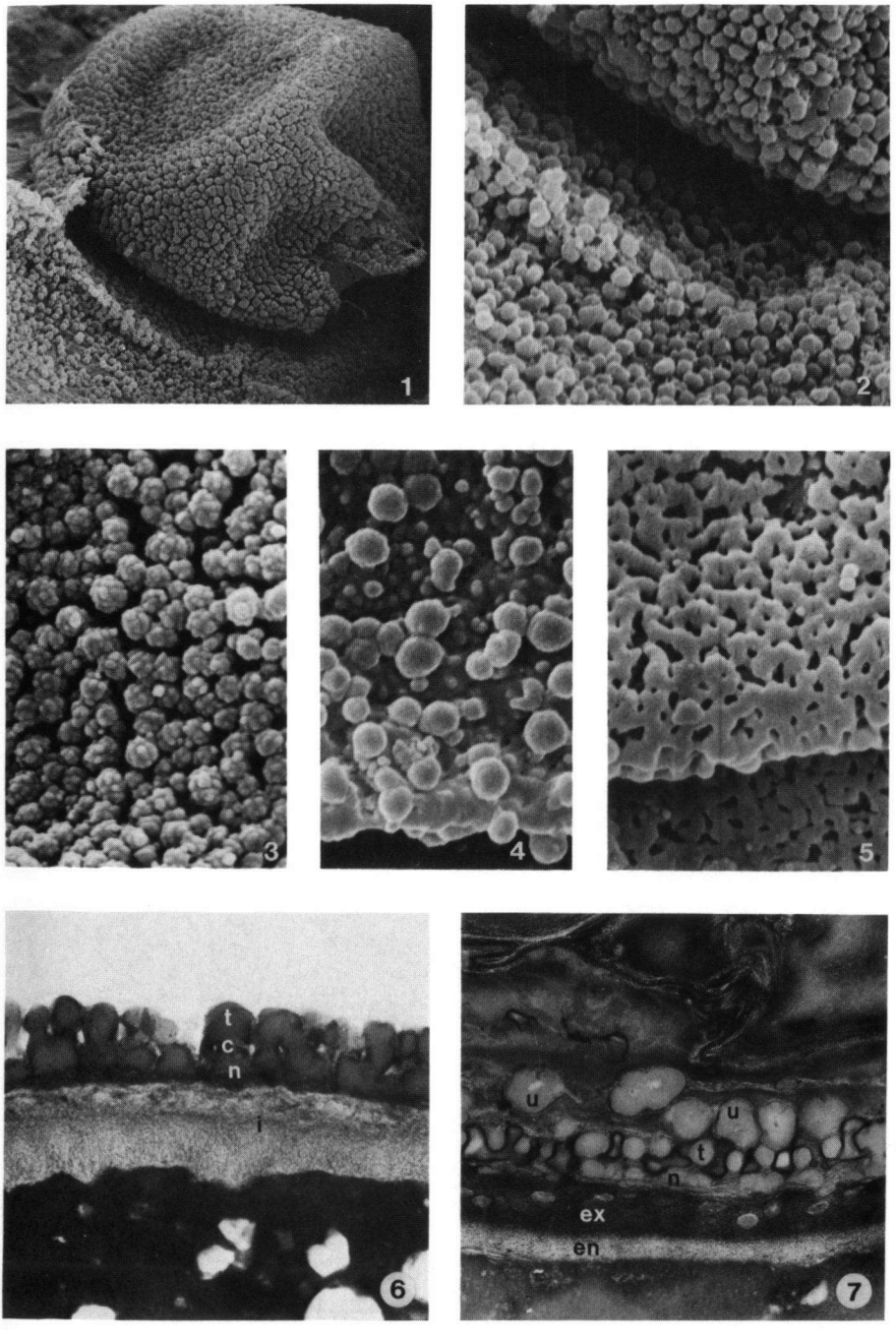


Plate 7. *Peliosanthes teta* (Convallariaceae).

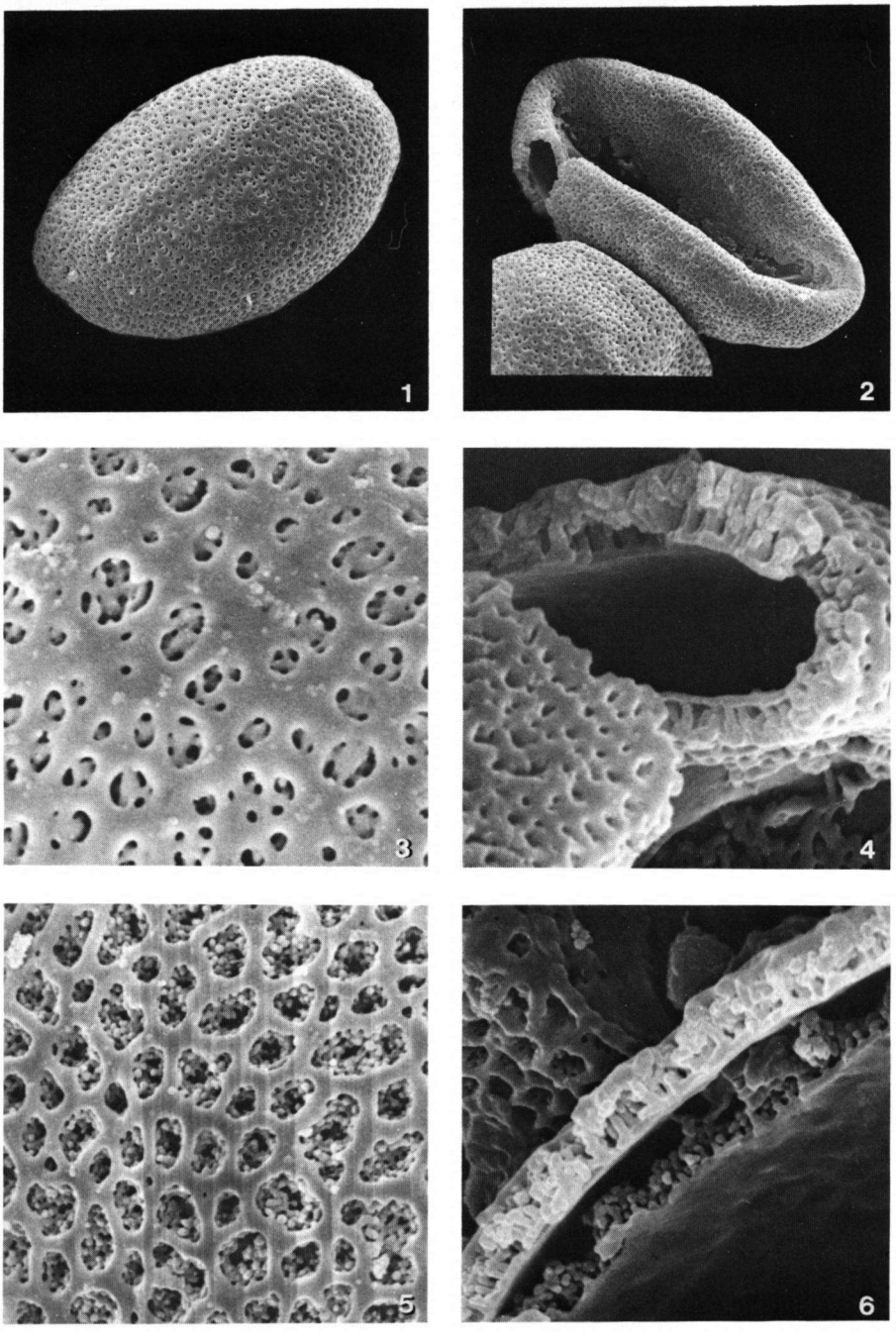


Plate 8. *Stemona phyllantha* (1–4), *kerrii* (5, 6).

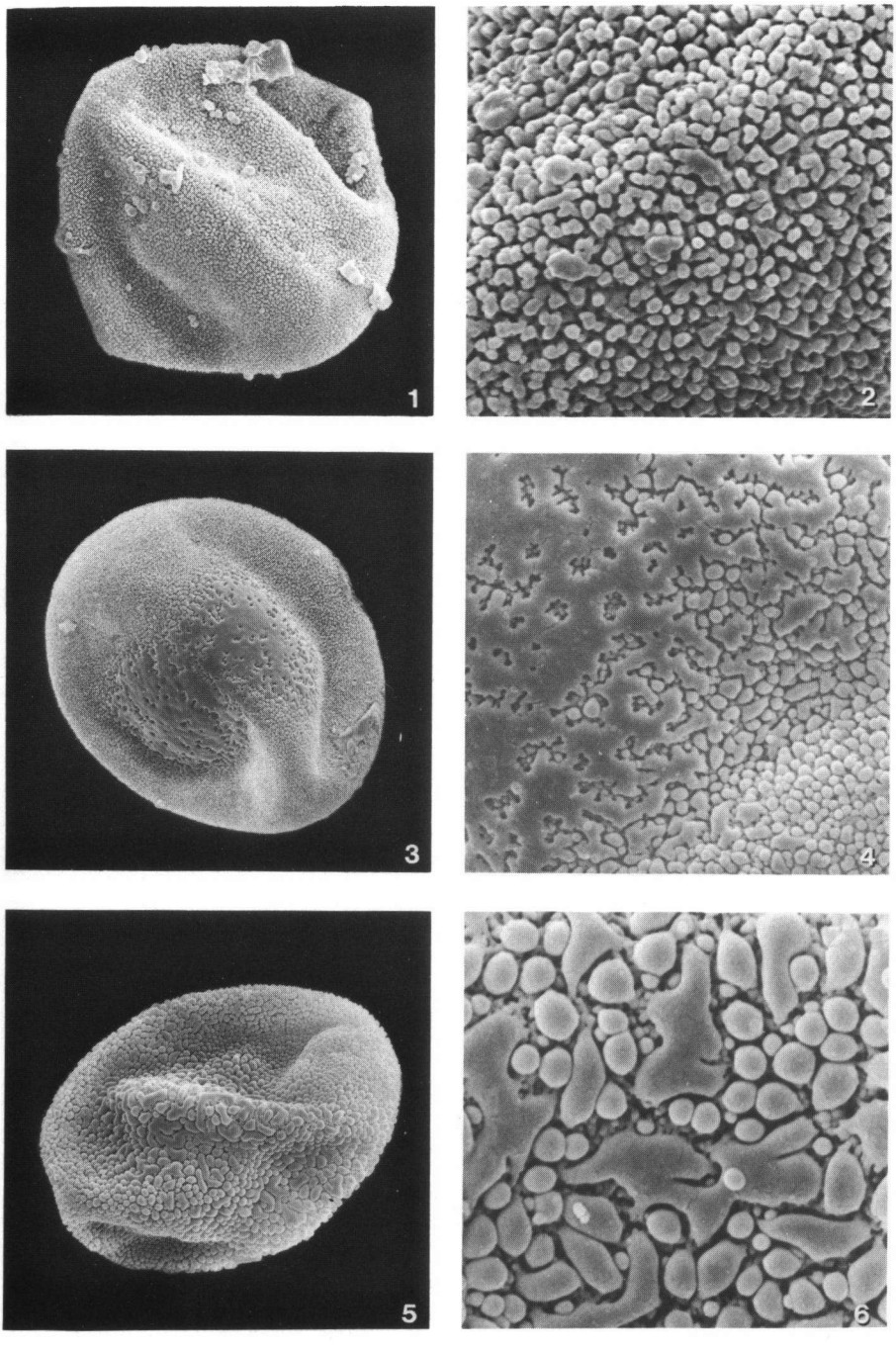
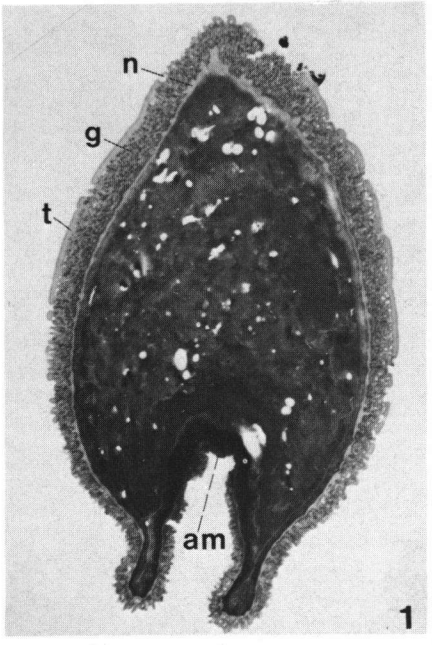
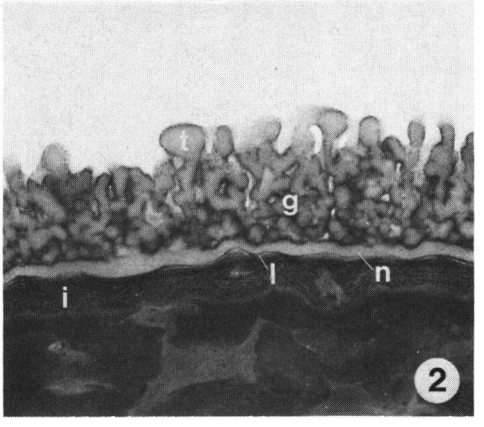
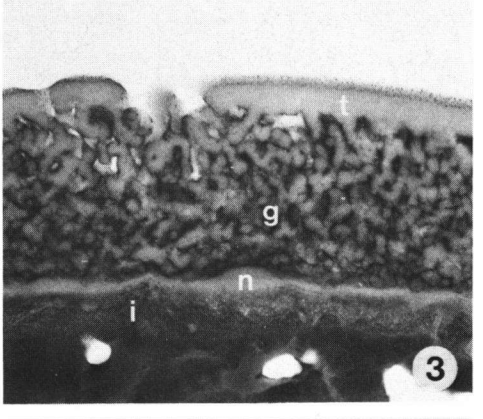
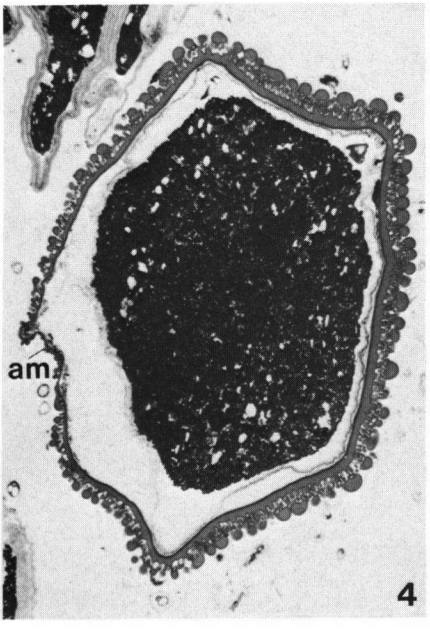


Plate 9. *Stemona parviflora* (1, 2), *japonica* (3, 4), *lucida* (5, 6).









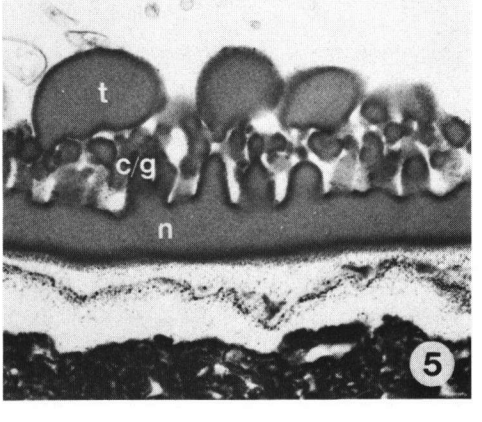


Plate 10. *Stemona japonica* (1–3), *lucida* (4, 5).

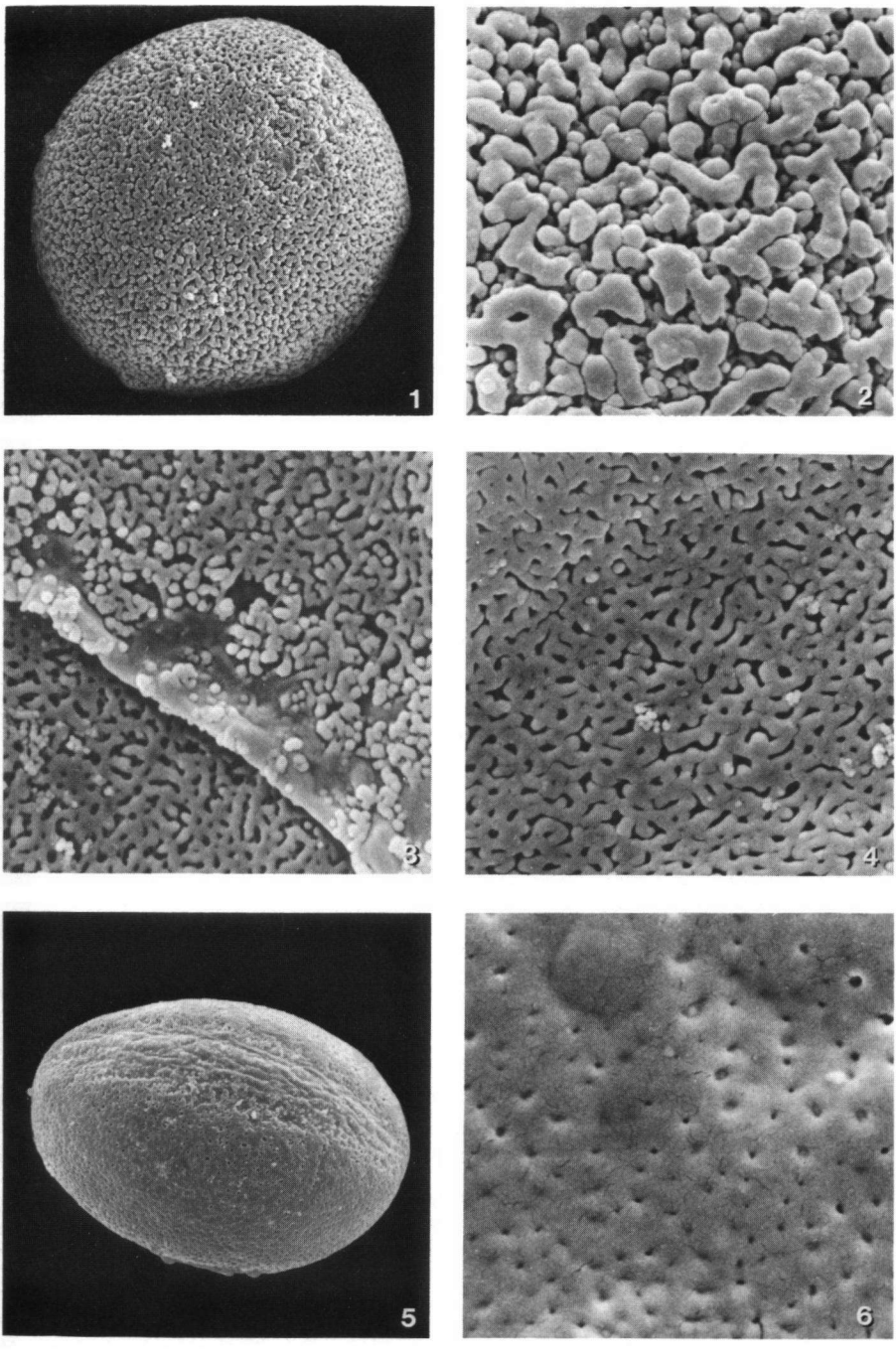


Plate 11. *Stemona tuberosa* (1, 2), *cochinchinensis* (3, 4), *wardii* (5, 6).

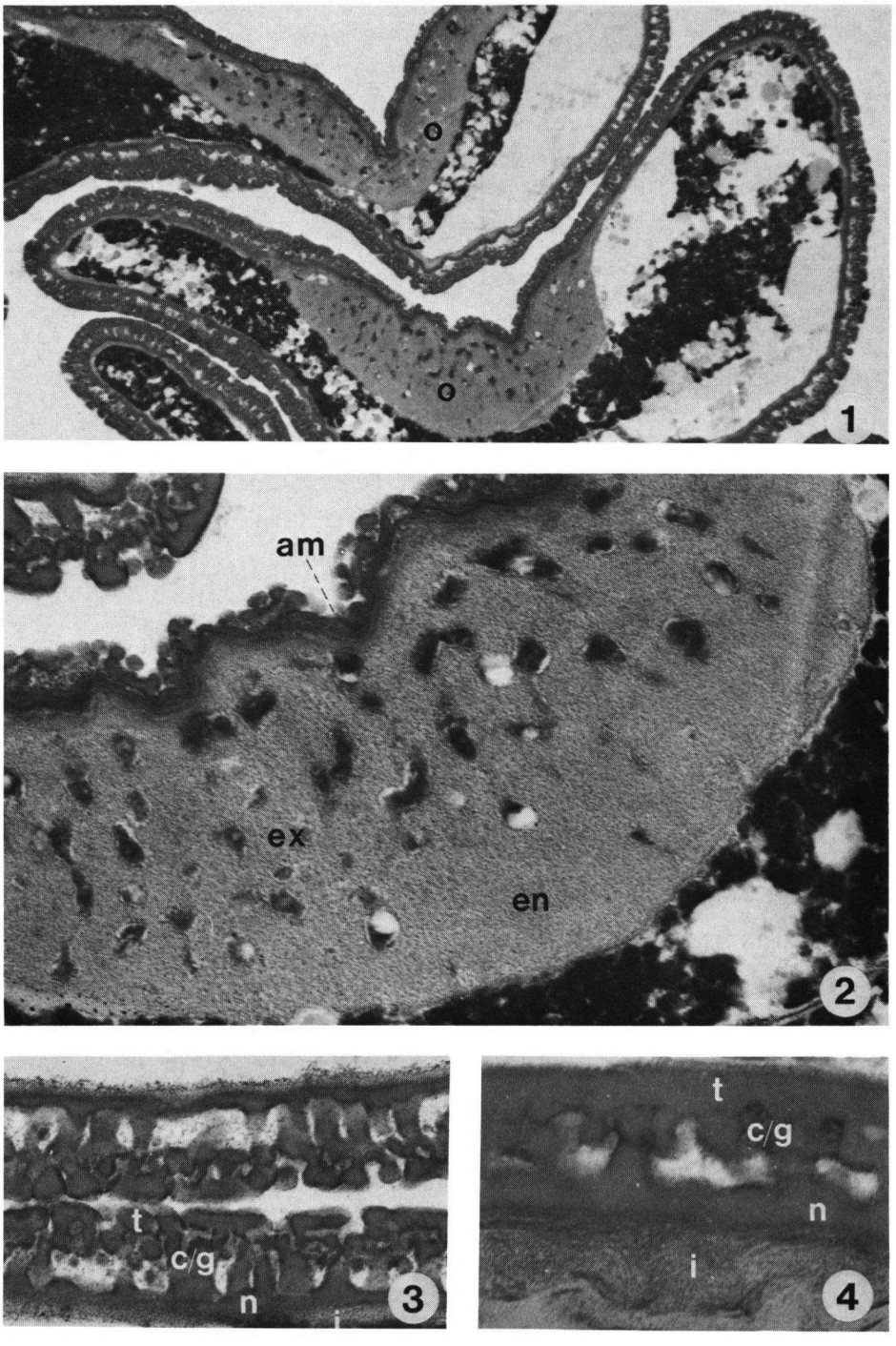


Plate 12. *Stemona curtisii* (1–3), *australiana* (4).

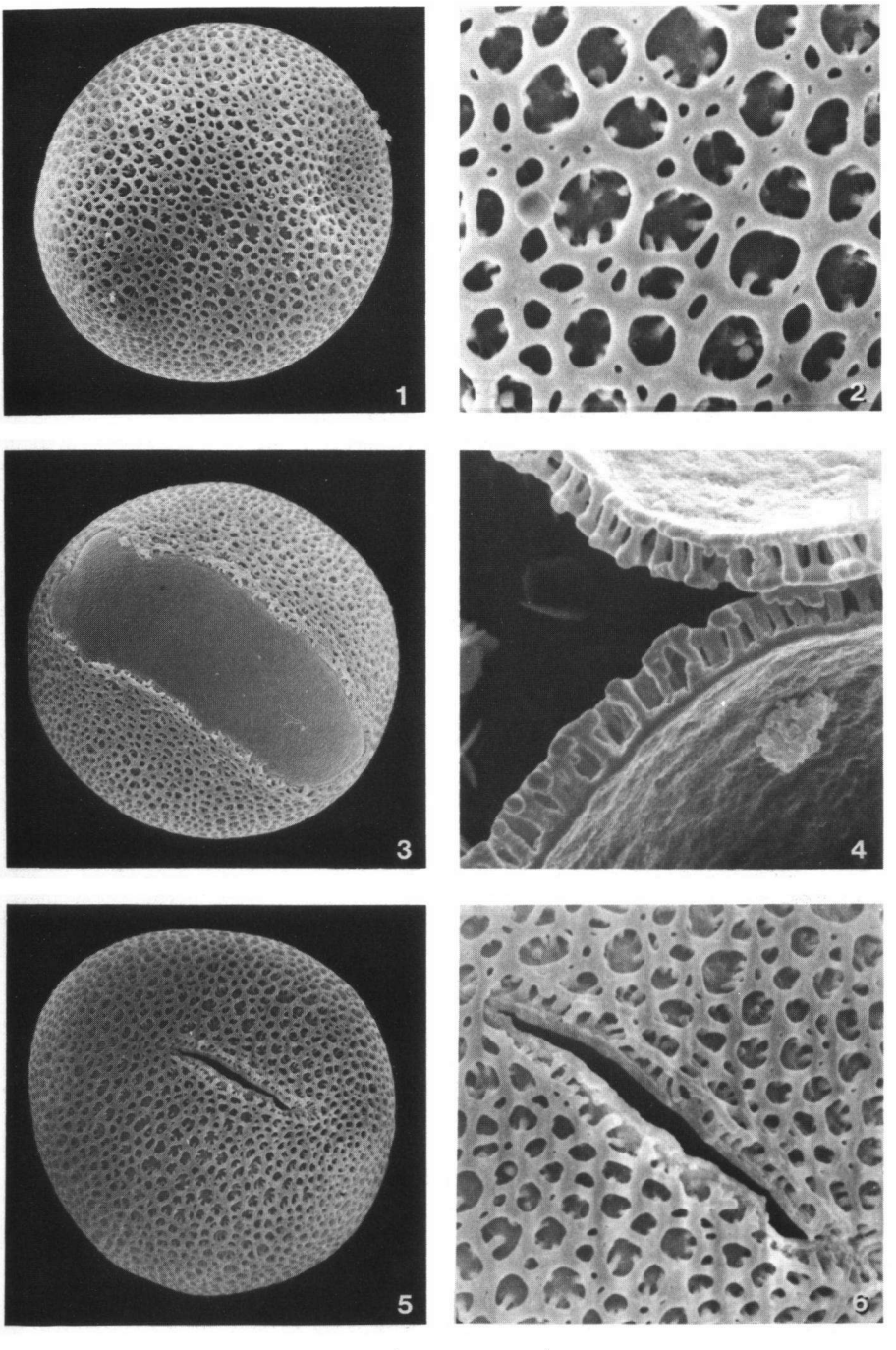
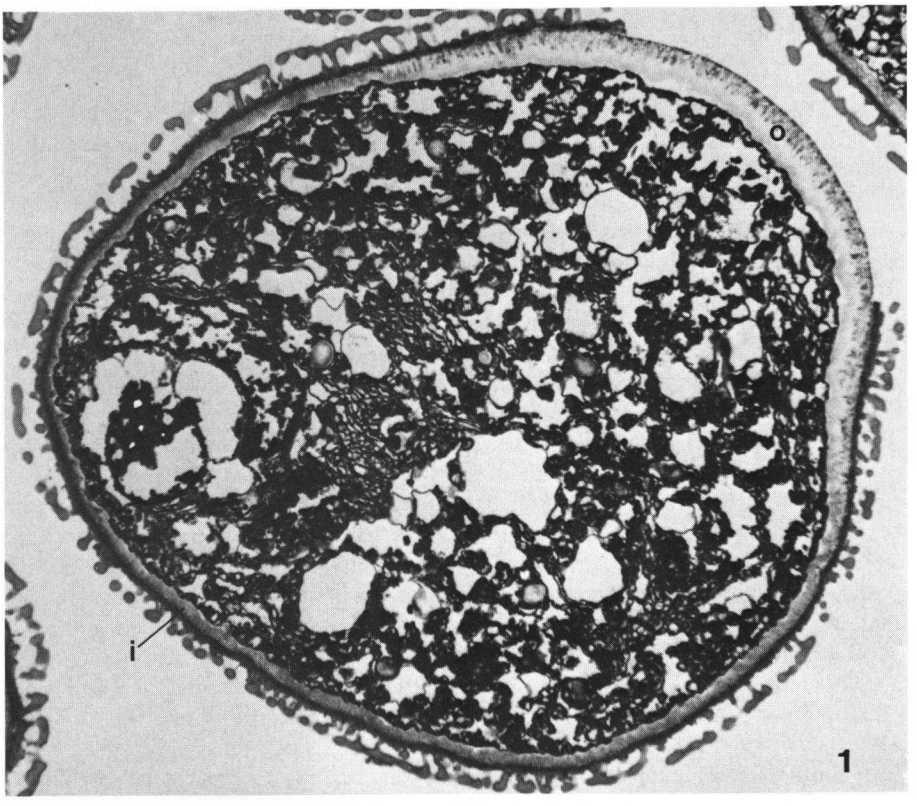


Plate 13. *Stichoneuron caudatum.*



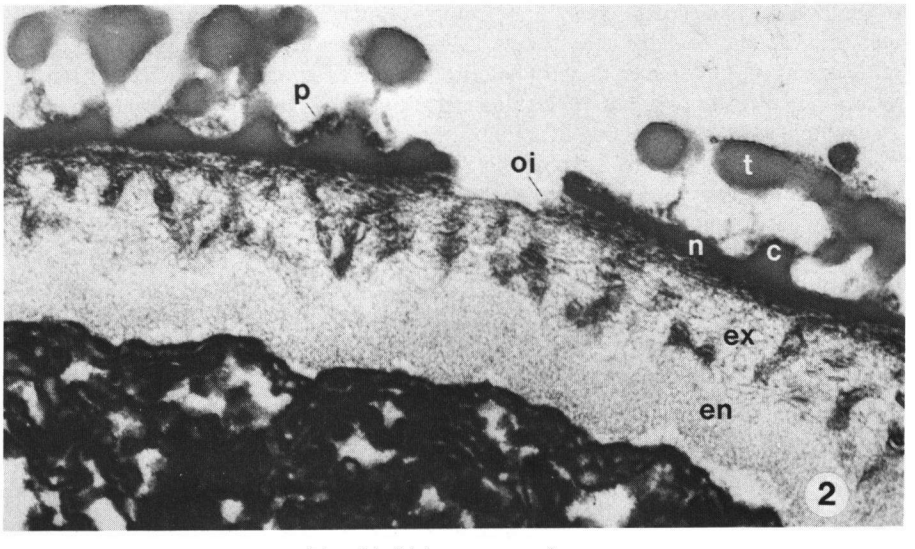


Plate 14. *Stichoneuron caudatum.*