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# A COMPARISON OF THE STRUCTURE OF OVULES AND SEEDS IN STEMONA (STEMONACEAE) AND PENTASTEMONA (PENTASTEMONACEAE)

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SUMMARY

*Stemona* and *Pentastemona* differ clearly in the size and structure of their ovules and seeds. Especially the development, shape, and cell wall thickenings of the endotestal cells, and by consequence the origin of the seed ridges, show marked differences. The embryological and seed anatomical characters support the proposal to give *Pentastemona* a family status.

## INTRODUCTION

The embryology of the small monocotyledonous family Stemonaceae (Roxburghiaceae) has been reviewed by Davis (1966) and more recently by Batygina et al. (1990); the seed anatomy of the family by Takthajan (1985). The family is mainly known from the detailed study by Swamy (1964) of *Stemona tuberosa*. *Stemona* is characterized by anatropous, bitegmic and crassinucellate ovules. The seed coat of *Stemona* is provided with longitudinal ridges, which originate by local, periclinal divisions of the endotestal layer. The embryology of the two other genera of the Stemonaceae, viz. *Croomia* and *Stichoneuron*, is insufficiently known. According to Tomlinson & Ayensu (1968) and Rogers (1982) the ovule of *Croomia pauciflora* is also anatropous and bitegmic. Huber (1969) gave a description of the seed coat of *Croomia*.

The newly described genus *Pentastmona* Steen. was placed by Van Steenis (1982) in the Stemonaceae because i.a. all four genera were said to share a surprisingly similar seed structure and a characteristic aril. He described the ovules of *Pentastemona* as anatropous, with two integuments, and the aril as an irregularly lobed vesicular body. The familial status of *Pentastemona* was questioned by Dahlgren et al. (1985). They found the genus highly distinctive, about as distinct as *Trichopus* or even *Tacca*.

In this paper the structure of the ovule and seed of *Pentastemona* is described in more detail and compared with that in *Stemona*. The current study is complementary to the recent contributions of Duyfjes (1991) on the general morphology, of Van der Ham (1991) on the pollen morphology, and of Van Heel (1992, present issue) on the flower morphology of the Pentastemonaceae and Stemonaceae.

## MATERIALS AND METHODS

Most material was supplied through the generosity of B.E.E. Duyfjes and W.A. van Heel, Rijksherbarium/Hortus Botanicus, Leiden. The following material has been studied:

*Croomia japonica* Miq.: *Hatusima 19946* (L).
*Pentastemona egregia* (Schott) Steen.: *Bogner 1724*, cult. Bot. Garden L and M. – *P. sumatrana* Steen.: *de Wilde & de Wilde-Duyfjes 20311* (L), *21399* (L).
*Stemona australiana* (Benth.) C.H. Wright: *Wightman 1063* (DNA). – *S. japonica* Franch. & Sav.: *Hortus Pekinensis 82.631*. – *S. javanica* (Kunth) Engler, *Beguin 2333* (L). – *S. prostrata* Telford: *Craven 5546* (L). – *S. tuberosa* Lour. var. *ternatensis* (J.J. Smith) Duyfjes: *de Wilde & de Wilde-Duyfjes 21411* (L).
*Stichoneuron caudatum* Ridley: *Corner 30503* (L); *Bogner 1789*, cult. Bot. Garden M.

The material was dehydrated in a normal butyl alcohol series, embedded in glycol-methacrylate, and sectioned at 5 μm. The sections were stained by periodic acid/Schiff's reaction with a toluidine counter-stain. Hand-cut or microtome sections were submitted to several histochemical tests: phloroglucinol/HCl, aniline sulphate, ruthenium red, nigrosine, iodine in potassium iodine, and Sudan IV.

The SEM studies were carried out by means of an ISI-DS 130 at 9 kV. Mature seeds were sputter-coated with gold-palladium for c. 3 minutes. Material of younger stages was dehydrated in an ethyl alcohol series and critical point-dried with $CO_2$.

## RESULTS

*Ovule structure in Pentastemona egregia* (Figs. 1, 4–7)

The ovules are bitegmic, anatropous, crassinucellate and measure c. 410 × 264 μm. Ovules in cross section almost round, with a slightly protruding raphe. At the time of fertilization the ovules already have some raphide idioblasts in the tissues of raphe and chalaza. In the funicle and raphe intercellular spaces develop between the epidermis and the subepidermal cells. A single, small, amphicribral bundle with differentiating xylem and phloem elements passes through the funicle and raphe and ends at the chalaza. The ovules are embedded in a slightly staining 'mucous' substance.

The outer integument is about 35 to 40 μm thick, and 2, locally 3, layers thick. At those sites there are small intercellular spaces. In cross section the inner layer counts 12 to 17 (mean 15) tangentially stretched cells. These cells are 25 to 60 μm wide (mean about 45 μm).

The inner integument is 20 to 25 μm thick, and consists of 2, locally 3, layers, but without intercellular spaces. The cells of both the inner and the outer layer are small, more or less isodiametric.

The micropyle is formed by the inner integument only. The endostome opening is in direct contact with swollen, pollen-conducting cells of the parietal placenta. The cells of the inner layer of both the endo- and exostome elongate radially and may divide periclinally. The aril is initiated at about the time of fertilization by the formation of intercellular spaces and by divisions of the dermal cells at the junction of funicle and raphe and of the neighbouring exostomal rim.

The mature embryo sac is probably of the *Polygonum* type, occupies over half the length of the nucellus and is mainly covered by the nucellar epidermis at its upper part. The nucellar epidermis remains entirely one-layered. Its apical cells become slightly stretched radially and papillate, but do not divide periclinally. The chalazal part of the embryo sac narrows in a way characteristic for many monocots and is surrounded by a hypostase-like structure showing distinct cell wall thickenings. The basis of the embryo sac is connected with the chalaza by an axial strand of nucellar cells, which is surrounded by radiating 'cortical' cells. These cells elongate radially and may divide one or more times periclinally.

The ovules of *Pentastemona sumatrana* are similar in structure (figs. 2, 3, 8, 9). The megaspore tetrad is linear.

*Seed structure in Pentastemona sumatrana* (Figs. 10–16)

The seeds are about 950 to 1150 μm long and 750 to 900 μm in width (mean 1070 × 840 μm), and provided with 10 to 13 (mean 12) faint longitudinal ridges running from micropyle to chalaza. Owing to the transparency of the exotesta the ridges look more pronounced under the binocular microscope than when viewed by SEM. The embryo is relatively small, about 180 μm long and surrounded by copious endosperm. Raphe not visible from the outside. The raphe and chalaza have an insignificant vascular bundle almost without peripheral parenchyma and locally with some raphide cells measuring about 130 × 65 μm.

The aril has the appearance of a vesicular collar and covers about one third of the seed. The aril is composed of a one-layered epidermis enveloping only a single large intercellular space. The epidermal cells have slightly thickened outer cell walls and contain large compound amyloplasts mainly centred around the nucleus.

The seeds are endotestal. The inner layer of the outer integument is developed into a very characteristic layer, which determines the ridged outer surface of the seeds. As counted in cross section, the number of endotestal cells has not increased during seed development. In this plane, the endotestal cells appear U-shaped by the thickening of the radial and inner periclinal cell walls and by the incurvation of the thin outer periclinal walls. The radial walls vary in length from 140 to 230 μm (mean 195 μm) near the micropyle up to 270 μm. The inner periclinal cell walls vary from 90 to 120 μm (mean 100 μm). The thickening of the radial walls is more or less reticulate and tapers towards the periphery. The inner periclinal wall is more evenly thickened, has several differently staining layers, and is provided with narrow pit canals. The endotesta does not react distinctly with lignin-specific stains. At the incurvature of the endotestal cells the cells of the outer layer of the outer integument have stretched radially and may divide once, sometimes twice periclinally. The radial walls of the endotestal cells corresponds with the ridges of the seed. At these places the cells of the outer layer remain small and do not divide, so that the exotestal layer is only one to three cells thick and about 9 cells span one endotestal cell. Except for the slightly thickened outer wall, the cell walls of the exotesta are thin. The exotesta is fully transparent, not tanniniferous, and the cells contain some starch grains. As seen in length sections, the number of the endotestal cells has increased considerably. From chalaza to micropyle they are arranged in rows of about 60 cells. As a result the cells appear very small in longitudinal sections (mean height about 15 μm only).

During seed development, the inner integument does not increase in thickness. Its cells, especially those of the inner layer, follow the seed enlargement mainly by stretching, until they collapse. In the mature seed, the tegmen no longer shows a distinct cellular organization along most of its surface but is mainly present as a homogeneous cell wall layer, slightly reacting with cutine tests. This layer is present in a very early stage after fertilization, already before the cell wall thickening of the endotesta has begun. The tegmic layer originates from the outermost wall of the inner integument. Underneath the exotegmic wall a thin dark-staining layer of compressed tegmic and nucellar cells is present. Locally a wall layer between endotegmen and nucellus is present, probably mainly of endotegmic origin. Near the chalaza the slightly tanniniferous tegmen and nucellus may have retained their cellular structure and their interfacial wall layer.

After fertilization, the outer integument has overgrown the inner one, and closes over the endostome. In the mature seed the endostome forms a small plug above the embryo and consists of tanniniferous cells with somewhat thickened walls. The tegmic wall ends abruptly at the plug.

The endosperm fills the major part of the seed. The cells vary in size, are thin-walled, and contain various storage materials; starch grains mainly around the embryo and near the chalaza, aleuron grains as well as lipids being more generally distributed. There is no distinct outer layer. The cells surrounding the suspensor and the peripheral cells are somewhat smaller than the central ones, but differ only quantitatively in contents.

Around the embryo there is a small zone of disintegrating endosperm tissue.

*Ovule structure in Stemona tuberosa var. ternatensis* (Figs. 17–20)

The ovules are bitegmic, anatropous and crassinucellate, have a distinct raphe, and measure about 600 × 200 μm. Funicle and raphe contain a relatively large amphicribral bundle with ring- and spiral-xylem elements and a differentiated phloem, without a distinct bundle sheath, but surrounded by several layers of parenchyma. The chalaza becomes quite prominent by periclinal divisions of the parenchyma cells at the periphery of the vascular bundle. Raphal and chalazal parenchyma without distinct intercellular spaces.

Outer and inner integument 2-, locally 3-layered, about 20 and 15 μm in thickness, respectively. Cells of all layers more or less cubical or somewhat elongated.

The exostome does not protrude above the endostome. The endostomal opening is in direct contact with the pollen-conducting tissue of the placenta/funicle. Aril development starts with periclinal, later anticlinal divisions of dermal cells at the funicle and proceeds to the adjacent exostome rim. Aril initially without distinct intercellular spaces.

Nucellus large, composed of many small cells and without the radial cellular arrangement as in *Pentastemona*. Nucellar epidermis one-layered, the cells at its apex stretching radially and sometimes dividing periclinally. Embryo sac pear-shaped, probably of the Polygonum type, occupying about 1/3 to 1/4 of the length of the nucellus.

Raphe, chalaza and inner layer of outer integument with starch grains.

*Seed structure in Stemona australiana* (Figs. 21–39)

The seeds, excluding the aril, are about 7 × 4 × 4 mm and provided with distinct longitudinal ridges. The number of ridges varies within the species; mean number about 27 in *Stemona tuberosa*, 24 in *S. australiana*, and 18 in *S. japonica*. The ridges are less pronounced at the raphe. Embryo about 1.3 mm long. Seed coat without raphide cells. The exostome overgrows the endostome after fertilization. Endostome small, not tanniniferous and without thickened walls, still recognizable in the mature seed. Aril composed of many, at the funicle superimposed, locally flat or hollow hairs. Outer periclinal cell walls thickened, cells with very few small starch grains.

The seeds are endotestal. The outer and inner layer of the outer integument are multiplicative and develop longitudinal ridges. Inner layer dividing several times periclinally, forming radial rows of about 10 cells high at the ridges and 2 to 4 cells at the grooves. In cross section each ridge formed by 2 to 3 cell rows. Walls of the endotestal cells slightly thickened, more or less reticulate, and with small less discrete pits. Endotesta only slightly ligniferous. No distinct inner layer of the testa. Two innermost layers of the endotesta more tangentially stretched.

Endotestal ridges become somewhat flattened by an opposite division pattern of the exotestal layer. Cells of the outer layer small, more or less cubical and one-layered at the top of the ridges, but radially stretching and dividing periclinally at the grooves. At the flanks of the ridges, between the exo- and endotestal cells, intercellular spaces may develop. Exotesta tanniniferous. Exotestal cells at the top of the ridges longitudinally stretched, about 3 to 4 times their width, the cells at the flanks of the ridges polygonal. Outer periclinal cell walls and the adjacent parts of the radial walls of the exotesta thickened. The peripheral layers of raphe and chalaza show the same development as the integumentary part of the testa.

Tegmen not multiplicative. Cells of the outer layer with slightly thickened outer periclinal wall, stretched tangentially and longitudinally and mostly compressed in the mature seed. Inner layer of the tegmen somewhat tanniniferous, locally still recognizable, and with thickened inner periclinal wall. Nucellar tissue compressed or resorbed, except for some remnants near the chalaza.

Endosperm initially nuclear, later cellular. Cells of the endosperm radially arranged, more or less isodiametric and thin-walled. Peripheral cells somewhat smaller than the central ones. Outermost cell walls slightly thickened. Endosperm with amyloplasts of various size, aleuron grains and lipids. Endosperm around the embryo disintegrating and without storage material.

The seed coat anatomy of the various *Stemona* species may differ in detail: for instance, seed ridges in *S. japonica* as compared with *S. australiana* with more (about 10) rows of endotestal cells per ridge and with less manifest periclinal divisions of the outer layer at the furrows.

*Ovule structure in Stichoneuron caudatum*

The ovules are anatropous, bitegmic and crassinucellate, and measure about 360 × 250 μm. Raphe prominent with differentiated xylem and phloem elements. Outer and inner integument mainly 2-layered. Cells more or less cubical, except those of the inner layer of the outer integument, which are elongated in the radial direction.

The epidermal cells of the nucellar apex elongate radially and divide periclinally to form a small nucellar cap. Cells below the embryo sac with an arrangement comparable to that in *Pentastemona*. Endostome elongate, protruding far above the rim of the outer integument and in contact with the pollen-conducting multicellular trichomes of the funicle/placenta.

Adequately preserved seed material not available.

*Seed structure in Croomia japonica*

The general structure of the mature seed resembles that of *Stemona*. The raphe is less prominent, about the shape of a ridge, and has a bundle with differentiated xylem and phloem elements. The seeds have about 21 longitudinal ridges.

The ridges are less pronounced and originate by periclinal divisions of the endotesta. Each ridge is composed of 2 to 4 (mostly 2) rows of 4 to 5 cells high. Endotesta at the grooves only 1 or 2 cells in thickness. Innermost cell layer of the endotesta tangentially stretched. Endotestal cells slightly reticulately thickened. The outer layer of the testa is entirely one-layered and has not divided periclinally at the grooves as in *Stemona*. The walls of the exotestal cells are also slightly thickened. Intercellular spaces occur at the flanks of the ridges, between the exo- and endotesta. Both exo- and endotestal cells slightly tanniniferous. No raphide cells are present in the testa.

Tegmen better preserved than in *Stemona*. Two cell layers often still recognizable. The outer periclinal walls of the exotegmic cells are thickened and form a distinct continuous wall layer. Inner periclinal walls of the endotegmen thickened likewise and form a somewhat thinner, parallel-running wall layer. Locally remnants of the compressed nucellus are present.

The copious endosperm consists of radially arranged, isodiametric, thin-walled cells and is stored with starch and aleuron grains and lipids. The amyloplasts occur in both the peripheral and central cells of the endosperm.

## DISCUSSION

The similarity of the ovule and seed structure between *Stemona* and *Pentastemona* as posed by Van Steenis (1982) appears to be only a superficial one. The data from this study clearly show that *Stemona* and *Pentastemona* differ appreciably in the development and structure of their ovules and seeds. It is true that the ovules of both taxa may be described as anatropous, bitegmic, and crassinucellate, but these are the plesiomorphic character states in all angiosperms and hold true for the majority of the monocotyledons. Besides, the ovules show several differences in detail. The ovule of *Stemona* is bigger than that of *Pentastemona*, especially caused by a more pronounced development of the chalaza and the nucellar base.

The differences in the structure of the ovules are also expressed in the mature seeds. The seeds of *Stemona* are much bigger and have a well-developed raphe and chalaza. Moreover, the seeds show marked differences in the anatomy of their seed coats. Characterization of seeds according to Corner's terminology, so successfully applied to the dicotyledons, appears often problematic in the monocotyledons because of the

presence of more than one mechanical layer in the seed coat. If one disregards the tegmic wall layer of *Pentastemona*, the seeds of both species may be characterized as endotestal. However, the development, shape and cell wall thickenings of the endotestal cells, and by consequence the origin of the seed ridges, are quite different.

In comparison with the dicotyledons, the monocotyledons have relatively many taxa with seeds provided with a number of longitudinal ridges. Ridged seeds are found in many taxa, at the family level for instance in Eriocaulaceae, Pontederiaceae, Stemonaceae, Taccaceae, Xyridaceae, and Zosteraceae, at the genus level in *Anigozanthos*, *Blancoa*, and *Conostylis* (Haemodoraceae), *Cyclanthes* and *Dicranopygium* (Cyclanthaceae), *Ctenanthe* (Marantaceae), *Navia* (Bromeliaceae), and *Philodendron* (Araceae), and at the species level in *Aponogeton* (Aponogetonaceae). The ontogeny as well as the anatomical structure of the ridges in the mature seeds may show considerable differences. Seed ridges must have originated several times during the evolution of the monocotyledons. The ontogeny of the seed ridges proceeds along different pathways. They may originate by the shape of cells of the outer layer of the outer integument (*Burmannia*, *Thismia*), by divisions of the endotesta (*Stemona*), by the shape of the endotestal cells (*Pontederia*), or by the shape of exotegmic cells (Xyridaceae, *Tacca*). The presence of the U-shaped endotestal cells in *Pentastemona* and their expression in the striate seed is strikingly paralleled by the situation in Pontederiaceae (Takhtajan, 1985).

Probably, seed ridges are functional in the dispersal of seeds. As compared with dicotyledons, monocotyledons have a relatively high proportion of aquatic or amphibious species. Many monocotyledons prefer wet environments and grow in, or at, rivers, lakes, pools, marshes, swamps, or in the understorey of forests (Arber, 1920; Cronquist, 1981). In these environments water plays an important role in the dispersal of seeds, and hydrochorous dispersal by means of drifting on water surfaces (nautochory) or by rainwash (ombrochory) generally is of frequent occurrence (Van der Pijl, 1982). In temperate wetlands even up to 70% of the species may have a hydrochorous dispersal (Bouman, personal observation). Next to the small size, low specific weight, repellent surfaces, and special devices such as floating tissues, ridges on the seeds may promote floating by enlarging the surface and capturing air bubbles between the surfaces of seed and water. This may especially be effective in small to medium-sized seeds.

No data are available on the type of dispersal in Pentastemonaceae and Stemonaceae. Due to the presence of distinct arils zoochorous dispersal seems probable. Huber (1969) and Dahlgren et al. (1985) suggested myrmecochory for *Stemona* and *Croomia*. However, diplochory, including hydrochory, must not be ruled out.

In spite of a number of differences in the seed anatomy of *Stemona* and *Croomia* recorded by Huber (1969), according to our own observations these genera (and probably *Stichoneuron* also) share the same basic seed coat structure, viz., a ridged (striate) testa which originated by periclinal divisions of the endotestal layer. Also the statement of Huber (1969) that Stemonaceae are characterized by a crosswise orientation of the outer and inner testal layers ('Kreuzschichtung') is not confirmed. Although the cells of the inner endotestal layer are elongated tangentially, only the exotestal cells at the apex of the ridges are somewhat longitudinally stretched in *Stemona*.

Regrettably, in view of the substantial variation in seed structure and by lack of detailed data it is not justified for the moment to compare the ovule and seed structure with those of possibly related taxa from the so-called para-Dioscoreales such as *Trichopus* and *Stenomeris*. Most members of the Dioscoreaceae have a cystalliferous endotesta, Taccaceae a well-developed exotegmen.

In conclusion, the differences in the structure of ovule and seed between *Stemona* and *Pentastemona* reported here support the suggestion of Dahlgren et al. (1985) and the implementation by Duyfjes (1991) to rank *Pentastemona* as a separate family.

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## EXPLANATION OF THE PLATES (Figures 1–39)

Plate 1. 1–7. *Pentastemona* ovules (LM). – 1: *P. egregia*, transmedian longitudinal section, × 170. – 2 & 3: *P. sumatrana*, median longitudinal section and detail of aril of developing seed, × 145 and × 90 respectively. – 4–7: *P. egregia*, cross section of ovary and cross sections of ovules at the level of the funicle, micropyle and embryo sac, × 45, × 350, × 245, × 160 respectively.

Plate 2. 8–16. *Pentastemona sumatrana* developing and mature seeds (LM and SEM). – 8: Group of developing seeds, showing aril, funicle and micropyle, × 20. – 9: Developing seed lateral view, × 55. – 10–12: Cross sections of the seed coat showing endotesta and tegmic remains, × 110, × 650, × 200 respectively. – 13 & 14: Longitudinal sections of a developing seed coat and mature seed coat showing detail of endotestal cell wall thickening, × 210 and × 330 respectively. – 15: Cross section of fruit with seeds, × 14. – 16: Cross section of seed showing U-shaped endotestal cells, small raphal bundle and endosperm, × 80. — a = aril, en = endotegmic wall layer, ex = exotegmic wall layer, h = hilum, m = micropyle, r = raphide cell, v = vascular bundle of the raphe.

Plate 3. 17–24. *Stemona tuberosa* developing seeds (LM). – 17 & 18: Transmedian and median longitudinal sections during nuclear endosperm stage, × 30. – 19: Cross section at the level of funicle/raphe showing aril development, × 100. – 20–23: Cross sections of developing seed coats, showing multiplicative outer integument, development of the ridges, tegmen and adjacent nucellar tissue, × 180, × 360, × 185, and × 90 respectively. – 24: Cross section of a developing seed during the cellularization of the endosperm, × 20. — a = aril, v = vascular bundle.

Plate 4. 25–31. *Stemona australiana* mature seeds (LM). – 25: Longitudinal section through the micropylar half of the seed, showing embryo, endosperm and aril, × 12. – 26 & 27: Cross section of the fruit and detail showing preformed rupture zone, × 8 and × 25 respectively. – 28 & 29: Cross section of the seed coat and detail of longitudinal section showing 2-layered tegmen, × 30 and × 130 respectively. – 30: Cross section through the raphe, × 40. – 31: Detail of a ridge, × 160. — i = intercellular space, v = vascular bundle.

Plate 5. 32–39. *Stemona australiana* ovules and seeds (LM and SEM). – 32: Ovules on the basal placenta with development of the aril, × 30. – 33 & 34: Mature seeds lateral and raphal view, × 8 and × 7 respectively. – 35 & 36: Seed coat ridges, × 30 and × 110 respectively. – 37: Aril, × 18. – 38 & 39: Sagittal view and cross section, × 220 and × 740 respectively, showing tegmic remnants. — it = inner layer testa, en = endotegmen.

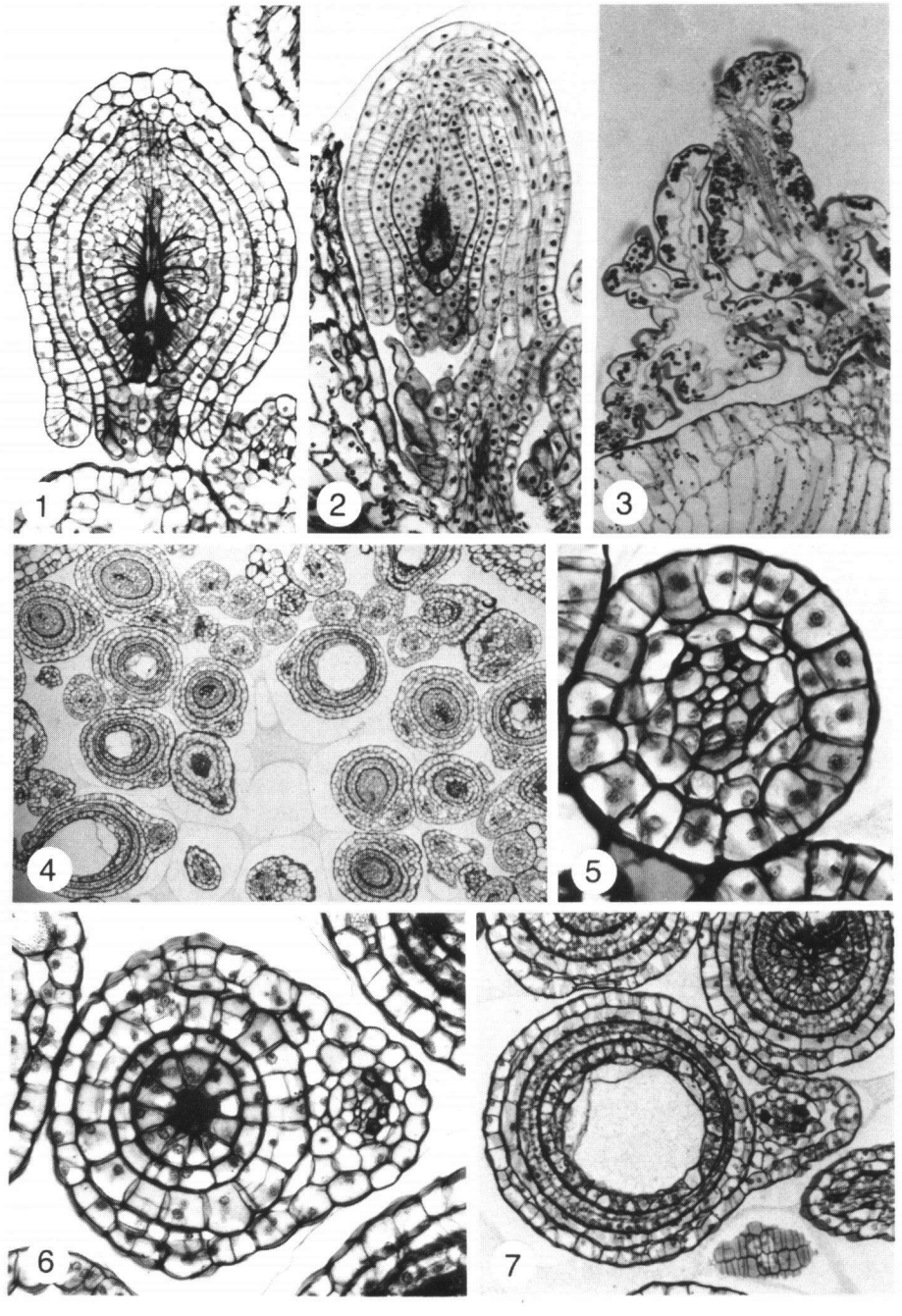


Plate 1 (Figs. 1–7; legend on page 509)

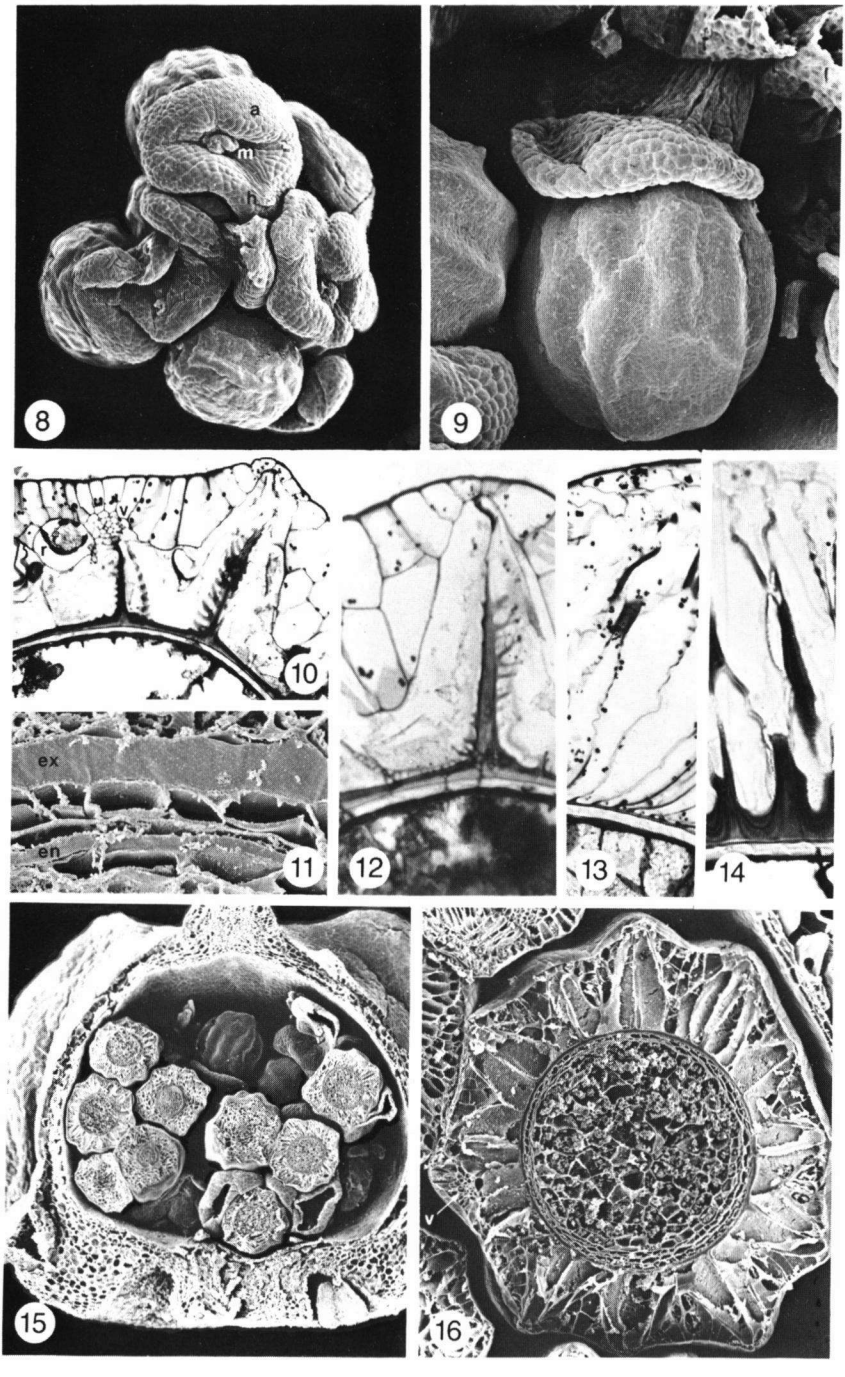


Plate 2 (Figs. 8–16; legend on page 509)

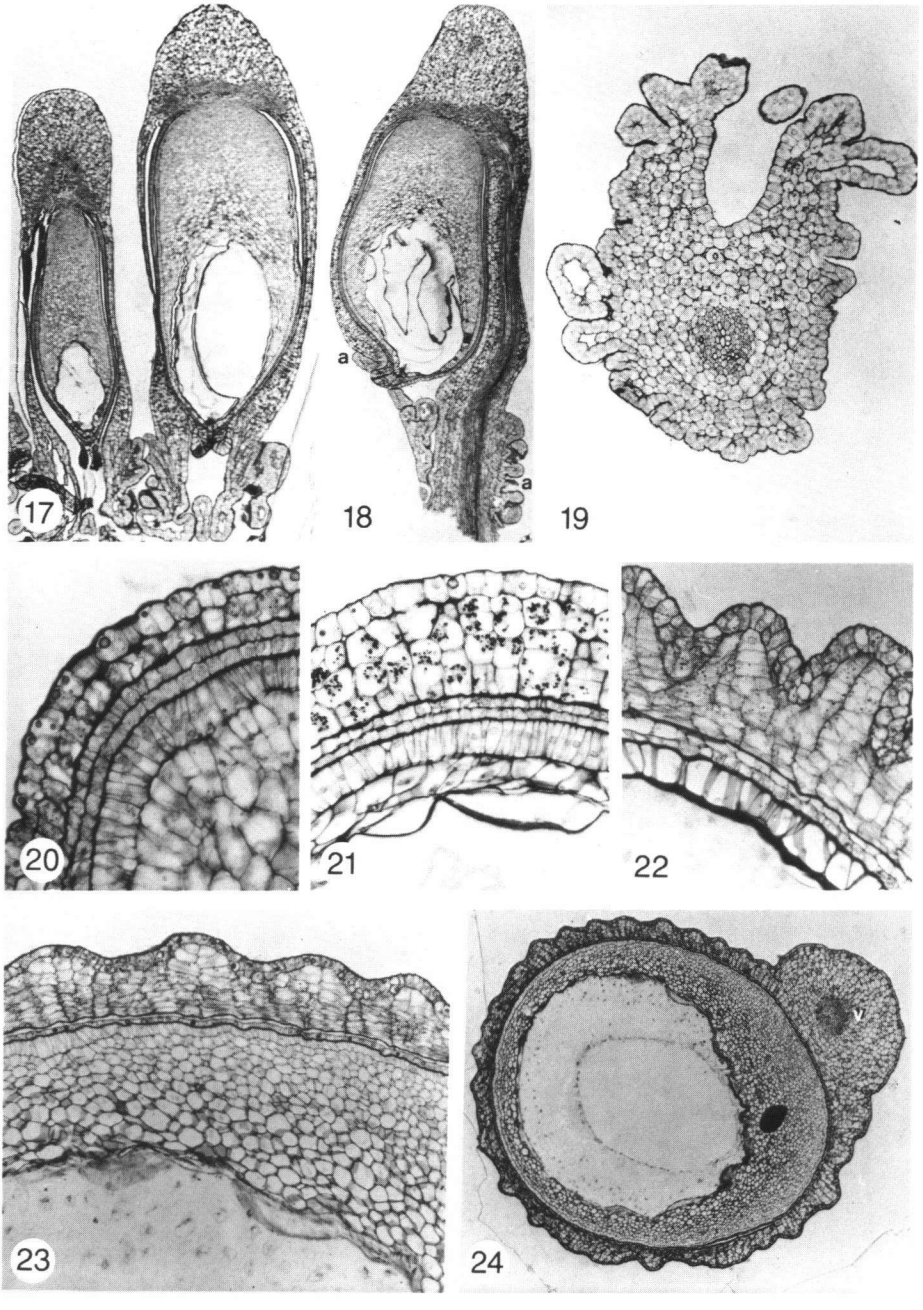


Plate 3 (Figs. 17–24; legend on page 509)

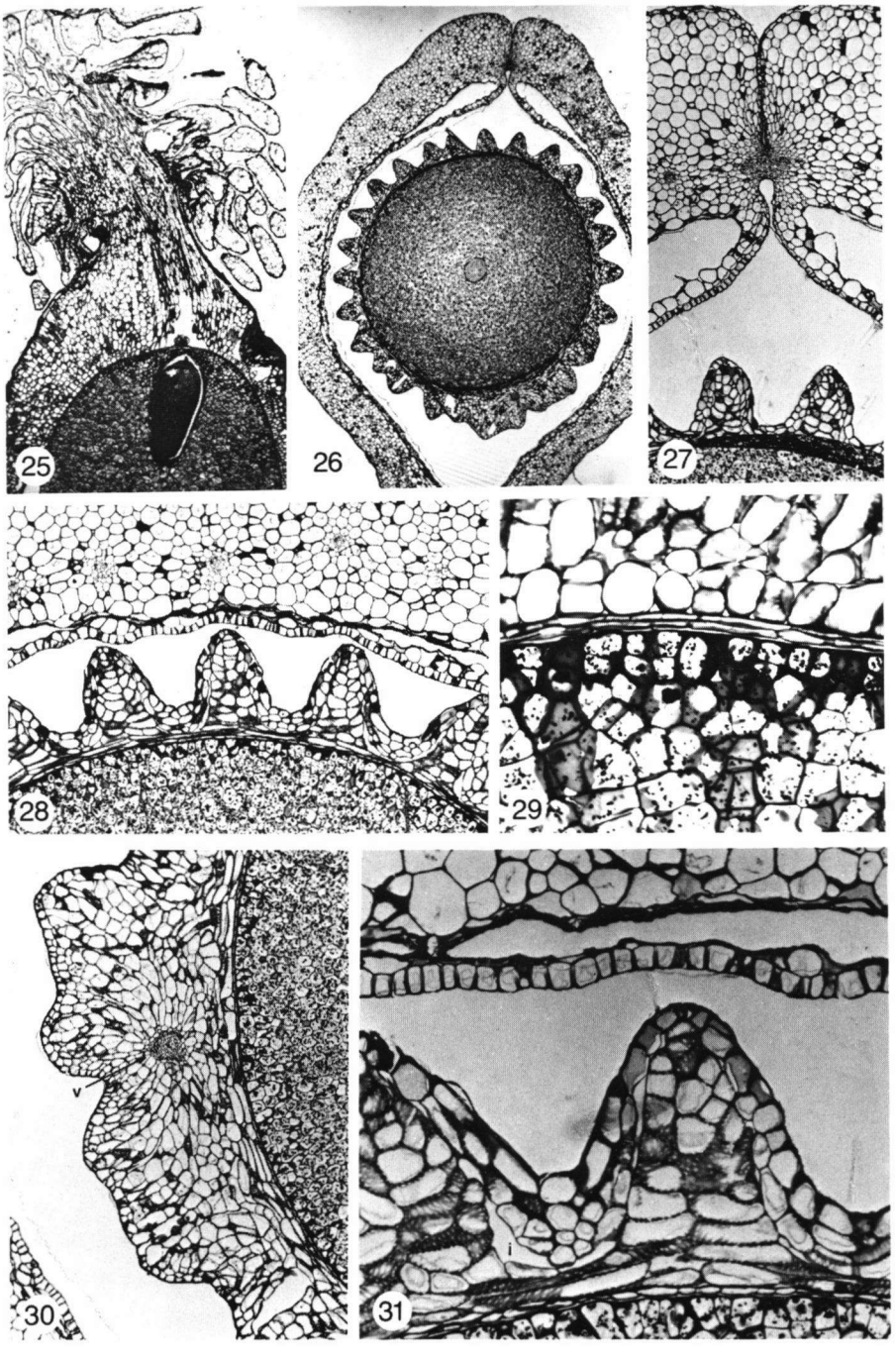


Plate 4 (Figs. 25–31; legend on page 509)

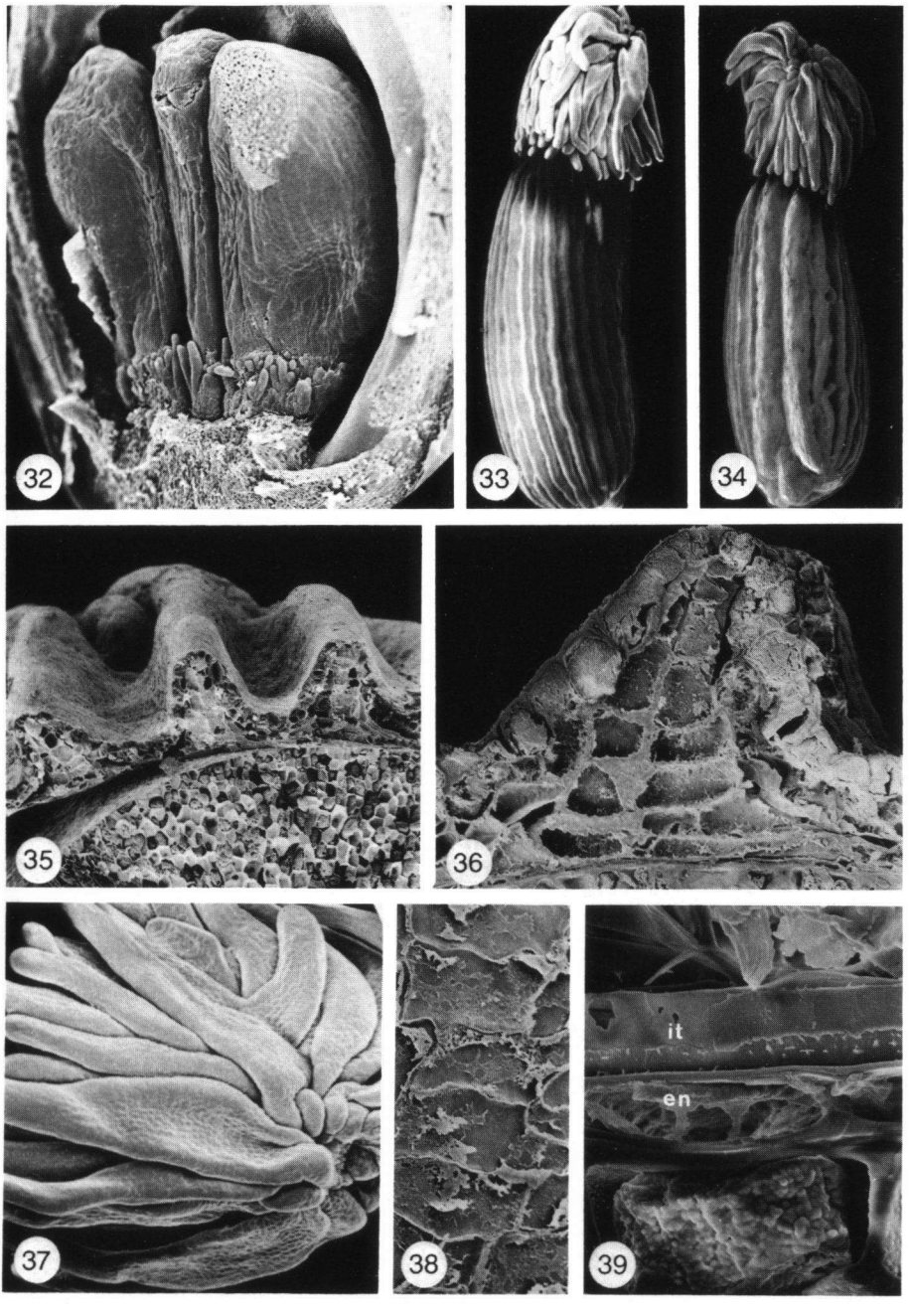


Plate 5 (Figs. 32–39; legend on page 509)