

## OVULE ONTOGENY AND SEED DEVELOPMENT IN *POTAMOGETON NATANS* L. (POTAMOGETONACEAE), WITH A NOTE ON THE CAMPYLOTROPOUS OVULE

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### SUMMARY

The ovule of *Potamogeton natans* is crassinucellate, bitegmic and ortho-campylotropous. Both integuments are dermal in origin and develop by intercalary growth. The seed coat consists of the compressed layers of the integuments, of which only the outer layer shows cell wall thickenings. The campylotropous curvature differs from the usual types and is brought about by a proliferation of the adaxial carpel wall. The terminology, structure and functional aspects of the different ovule types are discussed.

### 1. INTRODUCTION

An inflorescence of *Potamogeton* consists of spirally arranged flowers which are born almost at right angles to the axis of the inflorescence and are sometimes subtended by bracts. Each flower has four stamens and uni-ovulate carpels in alternate position, as indicated clearly by POSLUSZNY & SATTLER (1974). The scale-like protuberances (tepals) inserted on the connective of the mature stamens are initiated before, and mostly spatially separated from, the corresponding stamens.

*Potamogeton* already was a research object of such early plant embryologists as SCHLEIDEN (1839), SCHACHT (1850) and HOFMEISTER (1861). However, the literature on its embryology is still rather incomplete and mainly concerns embryo sac development and embryology (WIEGAND 1900; HOLFERTY 1901; COOK 1908; GUPTA 1934). Of the ovule ontogeny and seed coat development only fragmentary data are available. The most recent summary of the embryological records has been given by DAVIS (1966; see also LAKSHMANAN 1970). The ovule is bitegmic and orthotropous (by various others said to be anatropous, campylotropous or camptotropous). The nucellus is crassinucellate and has up to 7 parietal layers. The megaspore mother cell forms after meiosis a linear or T-shaped tetrad or "triad". The chalazal megaspore develops into a *Polygonum* type of

embryo sac. Endosperm formation is helobial. The coenocytic micropylar chamber later becomes cellular, while the single nucleus of the chalazal chamber increases in size and finally degenerates. The embryogeny confirms to the caryophyllad type and the terminal suspensor cell becomes vesicular.

Both integuments are two-layered, their micropylar parts excepted. In the mature seed endosperm is absent. The curved embryo, containing starch and oil, directly lies against the seed coat. From the integuments only the outer layer of the outer integument remains clearly cellular, the other layers become unrecognizable and form a cuticular layer around the embryo (NETOLITZKY 1926).

The fruit structure has been studied by AALTO (1970). Each of the four uniovulate carpels develops into an indehiscent fruit; they do not fit readily into the customary fruit classifications. Histologically they are drupes, but morphologically they resemble achenes. The pericarp is differentiated into a one-layered exocarp, a mostly rather thin and fleshy, parenchymatous outer mesocarp, which in a part of the species has large intercellular spaces and acts as a floating tissue, a sclerified inner mesocarp comprising 1–18 layers of sclereids of different shape, and a one-layered endocarp of long and narrow cells with massively thickened cell walls. In practice the sclerotic part of the mesocarp and the endocarp *sensu stricto* together are called endocarp (ROTH 1977). The dorsal part of the endocarp has two approximate, longitudinal sutures, consisting of thin-walled, parenchymatic cells, along which the fruit opens to allow the emergence of the germinating seed. The awl-shaped part which is lifted up from the fruit is mostly called the dorsal lid. The bursting of the lid starts at the apex of the fruit, which causes the embryo to emerge with its cotyledon first.

The fruits are polychorous and dispersed by hydrochory or zoochory (KIRCHNER et al. 1908). In part of the species the fruits are able to float for a shorter or longer period of time. In other cases the fruits may persist on detached shoots until the latter decay. Fruits can pass the intestinal tract of both birds and fishes unhurt. Also epizoochorous dispersal by mud sticking to water fowl has been recorded.

The present study aims at an amplification of our knowledge of the reproductive structures of *Potamogeton*, especially as regards ovule ontogeny and seed coat structure.

## 2. MATERIAL AND METHODS

The material of *Potamogeton natans* L. was collected in the Botanical Garden, University of Amsterdam and fixed in Allen's modified Bouin fluid or in Craf III. For standard light microscopy, flowers at various developmental stages were dehydrated in a TBA series, embedded in paraplast, microtome-sectioned at 6 or 7  $\mu\text{m}$  and stained with Heidenhain's haematoxylin, safranin and fast green; young and mature seeds were dehydrated by means of a NBA series, embedded in glycol-methacrylate, sectioned at 5 or 7  $\mu\text{m}$  with glass knives and stained with the PAS reaction and Eastman's haematoxylin. For SEM studies, some material was dehydrated in an ethyl alcohol series, critically point-dried and

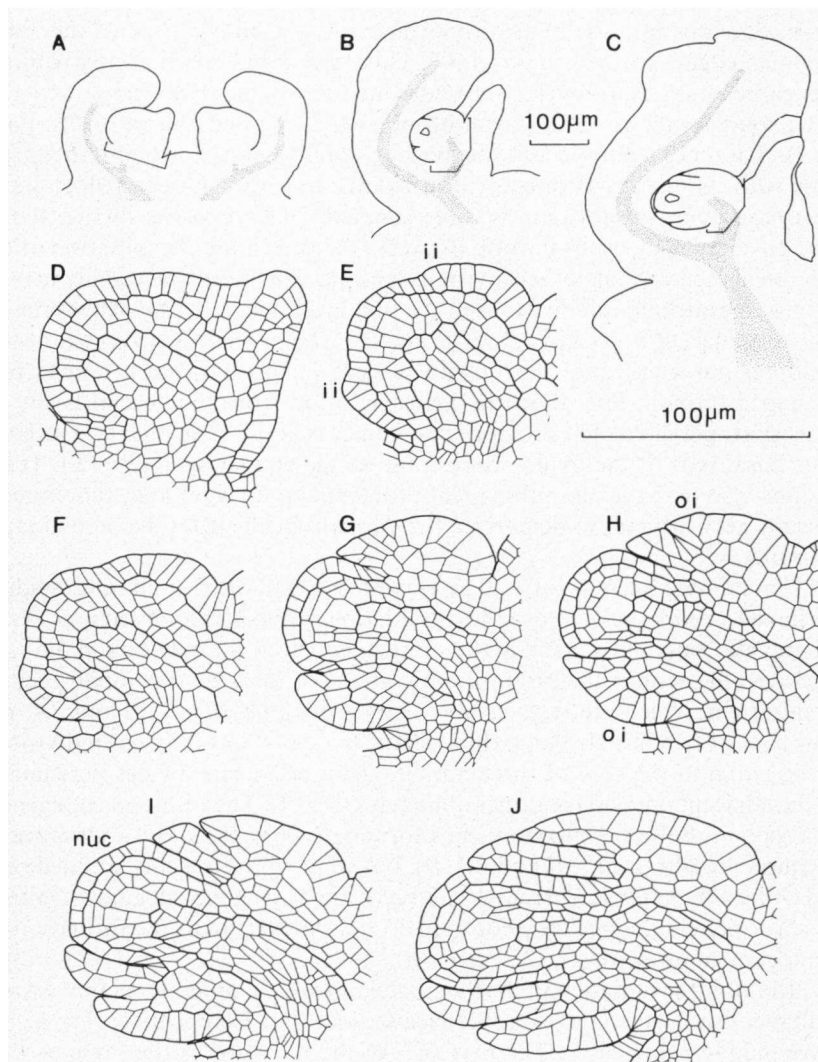


Fig. 1. Median longisections of ovules showing their relative position in respect of the carpel (A-C) and the initiation and early development of the integuments (D-J). Both integuments are of dermal origin. The curvature of the ovule gradually proceeds.

ii: inner integument; nuc: nucellus; oi: outer integument.

coated with gold; mature seeds were directly studied after coating.

### 3. RESULTS

The carpel primordia are obliquely cup-shaped, the dorsal side growing more rapidly and protruding the inner margin. The median part of the lower (inner)

margin develops into the ovule primordium. At the adaxial side of this inner margin an edge is formed (*figs. 1A–C*). This edge grows continuously with the other carpel margins to envelop the ovule and to form the stylar canal.

The young ovule is initially orthotropous and oriented almost horizontally (*fig. 1*). After megasporogenesis the ovule gradually bends down into the carpel locule with its micropyle directed downwards and becomes campylotropous. The young ovule primordium is three-zonated, i.e., it consists of two tunica layers enveloping a corpus portion (*fig. 1D*). A little before the initiation of the inner integument, periclinal cell divisions take place in the second layer concomitantly with anticlinal cell divisions in the first layer, whereby the ovule primordium develops (*figs. 1D and 2A*). The adaxial edge is slightly projected at this developmental stage, and the constituent cells of this part are arranged in a fan-shaped fashion, thus showing their derivation from the dermal layer. As in this part, periclinal cell divisions sometimes take place in the dermal layer of the basal part of the ovule primordium at the convex side (*fig. 1E*). These divisions also occur at the subsequent developmental stages and, therefore, it is usually very difficult to demarcate the derivative cells from the dermal layer at this side.

The inner integument is initiated as a slight swelling, the dermal cells dividing periclinally or obliquely. From the observation of median longisections, most probably the inner integument arises simultaneously at the convex and the concave sides. In sections the primordium consists of three or two initial cells of dermal origin, which are responsible for its growth (*figs. 1G, 2B and 3A, C*). In the case of two initials they exhibit either periclinal or oblique cell divisions (*fig. 3C*), and in the case of three initials, the median one divides periclinally and the adjacent ones divide rather obliquely (*fig. 3A*). The resultant cells generally divide in the same direction, thus forming two or three cell rows around the young nucellus (*figs. 1H and 3B, D*), but some of the apically situated cells divide bifacially (*table 1*). The subdermal cells underlying the integument initials also show periclinal divisions, but they do not participate in the formation of the integument proper (*figs. 1E, F and 2B*).

A little after the initiation of the inner integument, the outer integument arises simultaneously at the convex and concave sides, but it appears earlier at the convex side in some cases. The first sign of the initiation is the same as that of the inner integument (*figs. 1H, 2C and 3B, D*). The early growth is also due to divisions in two or three dermally originated initial cells (*figs. 1I and 3E, F; table 1*). As compared with the inner integument, two cell rows are of much more common occurrence than three rows; in other words: the outer integument is usually derived from two initials. However, three cell rows may sometimes originate in the following manner. After the first periclinal division of the outer of the two initials, the upper daughter cell divides anticlinally, thus rendering the integument primordium three-layered (*fig. 3G*). In this case the relative position of the inner cell in respect of the other derivatives is responsible for the difference in length of this row during the subsequent stages.

The bulk of the nucellus is formed by peri- and anticlinal divisions in the

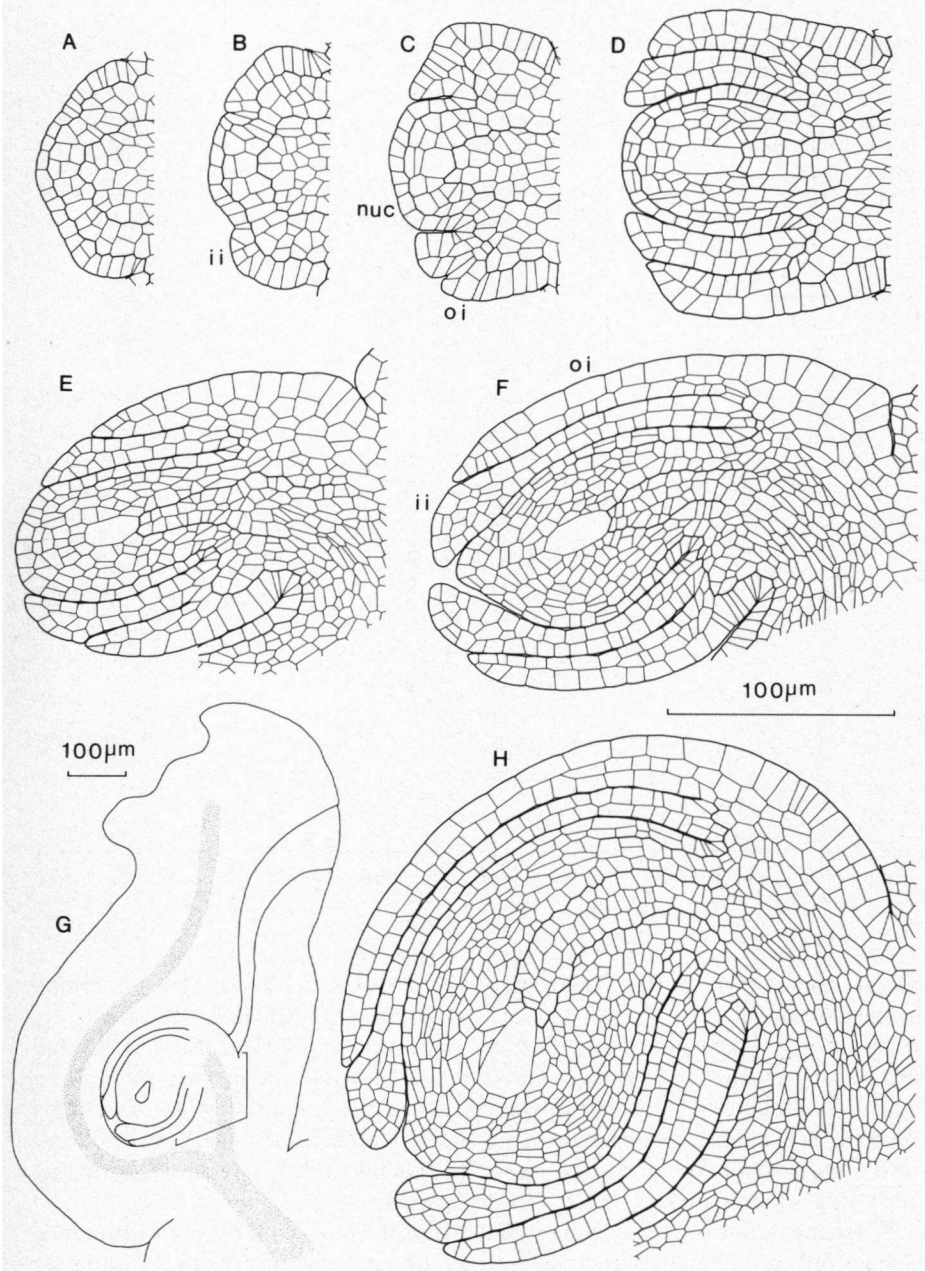


Fig. 2. Transversal longisections of ovules at the early stages (A–D) and median longisections at the later stages (E–H). The growth of the nucellus is mainly due to derivatives of the second tunica layer.

ii: inner integument; nuc: nucellus; oi: outer integument.

Table 1. Position of dividing or recently divided cells in the inner and outer integuments. Stages I–VII correspond to those of *figs. 1G, 1H, 1I, 1J–2E, 2F, 2H, 4B*, respectively. The numbers of ovules observed are in brackets. The numbers indicate the position from the apices of the integuments, but those in italics are from the base of the micropylar proliferation. Except for the cases in bold type figures, which are anticlinal, the others represent periclinal divisions in respect of the ovular axis.

		Stage I (14)		Stage II (15)		Stage III (18)		Stage IV (7)		Stage V (9)		Stage VI (21)		Stage VII (4)	
		cc	cv	cc	cv	cc	cv	cc	cv	cc	cv	cc	cv	cc	cv
II	il	1,1	–	1,1 1,2 3	1	1,1 1,3 3,4	1,1 1,2 2,2 4	2	1,1 5	3,6 6,7	1,1 2,6	3,7 8,10 10,13	1,5 6,7 8,11 11,12 12,12 13,13 14,15	8,18	1,4 15
		–	1,1	–	2	2	1,2 2,3	1,3 1	1,1	4	6,9	3,9 9,12	3,5 6,8 –9,9 9,10 12,12	20	17,41
		–	–	–	–	–	2	2	3	10,10 15	3,4 4,7	10	1,2 2,9 10,12 13,20 20	13,15	8
		–	–	–	–	–	2,3	4	–	8	6,6 7,8	5,9 14	6,9 8,12 12,12 14,19	–	16
		–	–	–	–	–	2,3	4	–	8	6,6 7,8	5,9 14	6,9 8,12 12,12 14,19	–	16
	ol	–	–	–	–	–	2,3	4	–	8	6,6 7,8	5,9 14	6,9 8,12 12,12 14,19	–	16
		–	–	–	–	–	2,3	4	–	8	6,6 7,8	5,9 14	6,9 8,12 12,12 14,19	–	16
		–	–	–	–	–	2,3	4	–	8	6,6 7,8	5,9 14	6,9 8,12 12,12 14,19	–	16
		–	–	–	–	–	2,3	4	–	8	6,6 7,8	5,9 14	6,9 8,12 12,12 14,19	–	16
		–	–	–	–	–	2,3	4	–	8	6,6 7,8	5,9 14	6,9 8,12 12,12 14,19	–	16

II: inner integument; OI: outer integument; il: inner layer; ol: outer layer; cc: concave side; cv: convex side of the ovule.

second tunica layer of the ovular apex (*figs. 1F–H* and *2B, C*). The subdermal archesporial cell is distinct at an early stage and soon divides periclinaly to form a primary parietal cell and the megaspore mother cell. The primary parietal cell undergoes further divisions to form a parietal layer. The megaspore mother cell undergoes meiosis; the micropylar cell of the dyad apparently fails to divide, because only triads were observed in our slides. The chalazal megaspore develops into a *Polygonum* type of embryo sac. The ovule is slightly flattened during the early stages (compare *figs. 1D, F, H, J* to *figs. 2A–D*).

After the initiation, every constituent cell of the inner and outer integuments divides only anticlinally to their surface (in the same direction as in the initials), thus increasing the length as well as the girth of the integuments (*table 1*), so that the inner and outer integuments retain their original thickness. In the case of three cell layers derived from three initial cells, however, cells of either the outer or inner layer (usually of the outer one) divide less actively and become

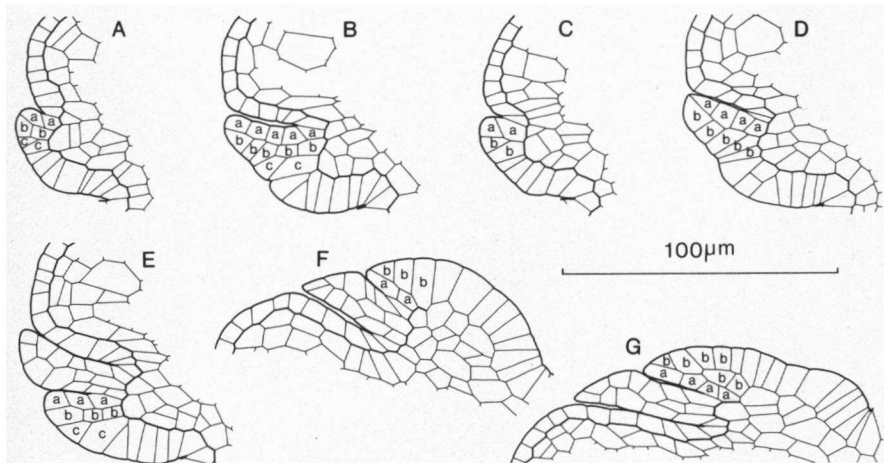
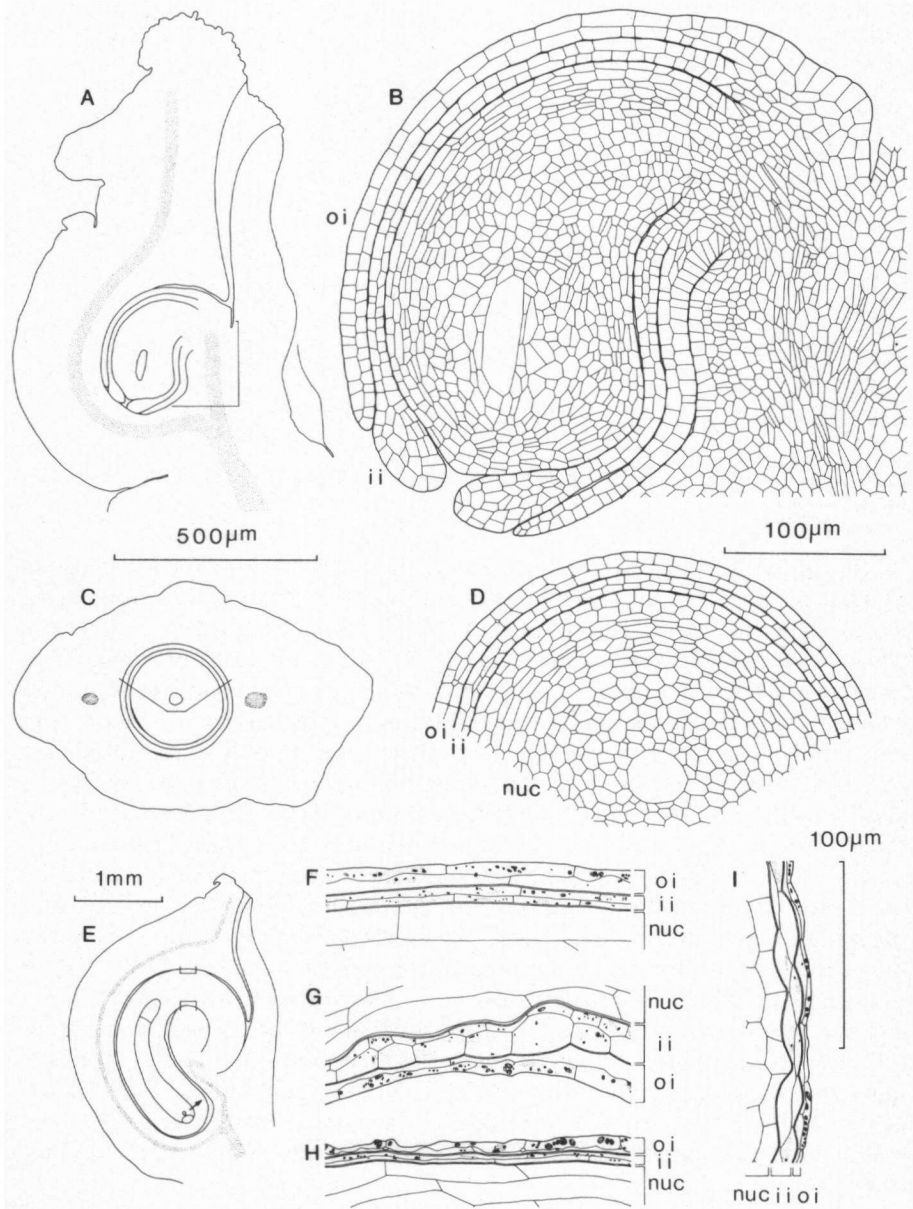


Fig. 3. Successive stages of initiation of the integuments. Derivatives of the same initials are indicated by the same letters.

surpassed by the other layers, thus making the upper parts of the integuments two-layered (*fig. 3B*; the inner integument at the concave side in *figs. 1I, J*). On the other hand, apically situated cells of the inner and outer integuments, when viewed in longisections, may cut off derivatives bifacially and contribute to the two-layered conditions as well. Serial longitudinal and cross sections indicate a retention of the three-layered condition (originated from three or from two initials) from the base upwards, but only rarely extending to the apical part (*figs. 2E, F, H*). The three-layered condition mingles with the two-layered one and is scattered all over the circumference of the inner and outer integuments, but is a little more frequently found at the lateral sides (*cf. fig. 4D*). The development of the integuments is mainly due to intercalary growth as indicated by the following points: (1) The two- or three-layered condition of the inner and outer integuments in developing ovules obviously results in two- or three-layered integuments in the mature or young seed, respectively (compare *figs. 2E, F*, to *figs. 2H* and *4B*); (2) As a matter of course, the growth of the inner and outer integuments in circumference results from anticlinal divisions in all constituent cells after their initiation; and (3) *Table 1* clearly shows that every cell of the inner and outer integuments is capable of dividing throughout the development of the ovule (in the case of a three-layered integument part, every cell of the middle layer also exhibits mitotic figures as do the cells of the inner and outer layers).

At the stage when the inner integument overgrows the nucellus, cells of the apical part of the inner integument begin to divide periclinally or in various planes (*figs. 1J* and *2D–F*). As a result, an endostome develops. The periclinal cell divisions are of more frequent incidence in the inner layer than in the outer one. About the same time, periclinal cell divisions also take place in the dermal layer of the nucellus. Although the divisions are most frequent at the nucellar



**Fig. 4.** Development of the seed coat. A–D: median longisections and cross sections of mature ovules; E: longisection of a fruit showing the curvature of a young seed; F, G: details of young seed coats indicated in E; H: seed coats at the later developmental stage (the same portion of F); I: cross section of young seed coats cut at the level of the arrow in E.  
 ii: inner integument; nuc: nucellus; oi: outer integument.



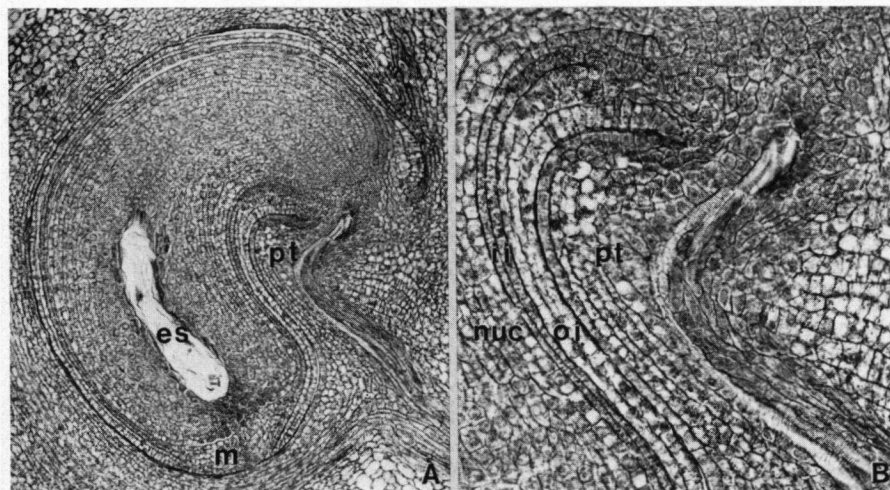


Fig. 5. Median longisections of a mature ovule.

A: the whole ovule ( $\times 100$ ); B: details of a part of A showing the proliferation from the adaxial wall of the carpel ( $\times 250$ ).

es: embryo sac; ii: inner integument; m: micropyle; nuc: nucellus; oi: outer integument; pt: proliferating tissue.

apex, they also occur at the flanks of the nucellus. The second tunica layer remains responsible for the greater part of the nucellar tissue (*figs. 1J and 2D-F, H*).

At the stage of pollination, the ovule faces the carpelary base, and completely fills the carpel locule. It is curved, pear-shaped in longisections and almost circular in cross sections (*figs. 4A-D*). Next to the curvature by about 90 degrees of the ovule itself, the curved shape is also the result of active periclinal cell divisions at the inside of the adaxial wall of the carpel (*figs. 4B and 5*). The resultant tissue begins to protrude into the median flank of the ovule. The micropyle is formed by the endostome alone, and the apical rim of the outer integument, which is tapering, lies at a rather far distance when viewed in longisections (*fig. 4B, cf. fig. 6A*). Although the inner and outer integuments become two- or three-layered by anticlinal cell divisions (*table 1*), their bases become four- or five-layered by periclinal divisions in every cell layer. The nucellus is relatively large. The nucellar cap has become three, and sometimes even five cells high, and the parietal layer may be as high as 6 cells. The corpus tissue running from the basis of the embryo sac to the chalaza is oriented in longitudinal rows, whereas the peripheral tissue of the nucellus is more radially directed (*figs. 4B, D*). The ovule is supplied by the rather massive ventral bundle of the carpel (*figs. 4A and 5*). This bundle turns completely into the ovule to fan out in the chalaza. A part of the xylem has already differentiated into ring or spiral elements.

The course of the pollen tube is porogamous. The pollen germinates on the stigmas and the tube(s) grows through the narrow stylar canal into the carpel locule. A pollen tube always arrives at the dorsal base of the ovule, from where

it grows in between the ovule and the carpel wall, seeking the shortest way along the lateral side of the outer integument, through the micropyle and penetrating the nucellar apex (*fig. 6A*). The cells around the ovular base deviate almost from the beginning from the other integumentary cells. Their cells are large and radially stretched, and they may divide periclinally.

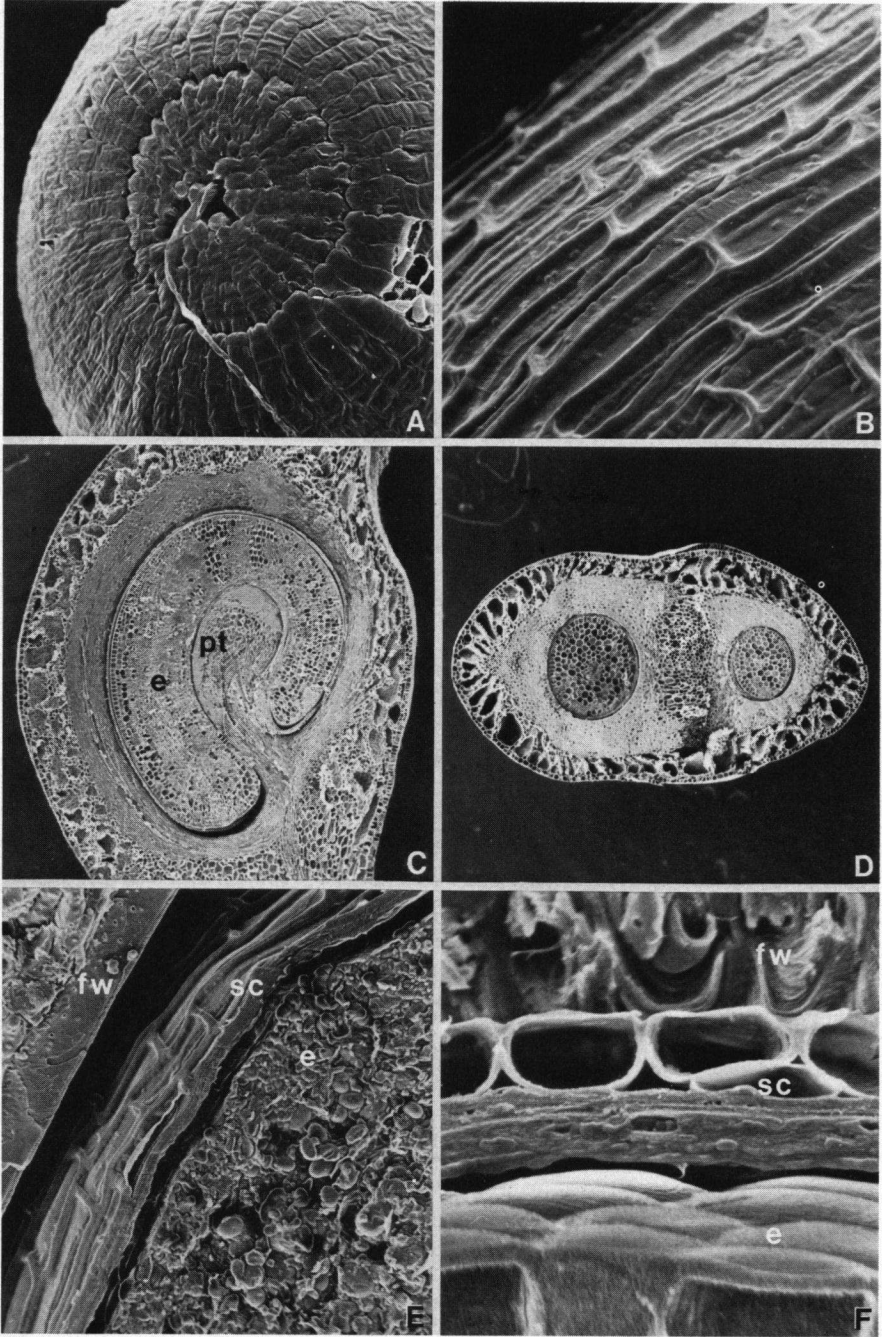
After fertilization the ovule grows considerably. The campylotropous curvature reaches to 270 degrees by the proliferation of the tissue of the adaxial carpel wall. Cells at both sides of the ventral bundle divide periclinally. The proliferated tissue forms a kind of central body around which the ovule has become curved (*fig. 4E*; cf. *figs. 6C, D*). The nucellus enlarges rather homogeneously, mainly by cell stretching. Especially the cells of the corpus tissue in the center of the nucellar base become very elongated, a small group of cells directly lying under the chalazal end of the embryo sac excepted. These cells do not enlarge, have aberrantly staining cell walls and seem to block the further expansion of the embryo sac downwards. During the first stages of seed development this tissue remains situated at about half-way the nucellus. The embryo sac first grows by stretching and by lysis of the surrounding nucellar cells (*fig. 4E*). Later the hypostase-like tissue is pushed aside and the embryo sac invades the basal half of the nucellus and gradually consumes the central part of the nucellus completely.

The integuments only grow in length, not in thickness. All cell layers stretch longitudinally (*figs. 4F, I* and *6B, E*) except for parts at the shorter, concave side and at the micropyle, where the cells may remain smaller (*Fig. 4G*). The anticlinal, and to a lesser extent also the inner periclinal, cell walls of the outer layer of the outer integument become thickened (*fig. 6F*). The anticlinal walls appear x-shaped in cross sections and are strongly pitted. The outer periclinal walls are thin and collapse at maturity (*figs. 6B, E*). The cells do not have specific contents except for some small starch grains. The inner and middle layers of the outer integument and every layer of the inner one become compressed and partly resorbed (*figs. 4H* and *6E, F*). Usually this proceeds from the apex to the base. The inner integument develops into a tanniniferous layer. The nucellar tissue is strongly compressed by the growing embryo (*Fig. 6F*). Cuticles are formed by the nucellar epidermis and the inner integument. The outer layer of the outer integument develops a thin cuticle and remains loose from the endocarp. Accordingly, the mature seed coat, although thin, is rather complex and formed by the exotesta, local compressed remnants of the inner and middle layers of the outer integument, a tanniniferous tegmen and a tightly packed layer of nucellar cell walls. Testa, tegmen and nucellus are separated from one another by cuticles.

The small chalazal-funicular part of the seed has developed a tenuous plexus

Fig. 6. Scanning electron micrographs of a mature ovule and seeds. A: micropylar part of the ovule with penetrating pollen tube ( $\times 270$ ); B: stretched cells of the exotesta ( $\times 390$ ); C, D: longi- and cross sections of fruits showing the campylotropous seed ( $\times 20$ ); E, F: longi- and cross sections of the seed coat ( $\times 240$ ,  $\times 960$  resp.).

e: embryo; fw: fruit wall; pt: proliferating tissue; sc: seed coat.



of ring and spiral tracheids. It is separated from the nucellus by a hypostase of about eight layers of small, tanniniferous cells with suberised walls. The hypostase is continuous with the tanniniferous tegmen. The peripheral parenchyma shows intercellular spaces. Most cells constituting the micropyle degenerate and are resorbed.

Endosperm formation precedes the embryogenesis. The endosperm is helobial. The micropylar chamber becomes coenocytic. The smaller chalazal chamber has one nucleus, which increases considerably in size. In the mature seed the endosperm has been fully consumed by the embryo. The mature embryo is curved over 270 degrees like the seed, and completely fills the embryo sac (figs. 6C, D). In cross sections the embryo is orbicular or suborbicular in outline. The cotyledon takes up about half of the embryo. The hypocotyl-root axis and the cotyledon are provided with a central provascular strand. The plumule contains several leaf primordia. The embryonal tissue is filled with starch and aleuron grains, except in the meristematic parts (Fig. 6E).

#### 4. DISCUSSION

Potamogetonaceae have many advanced characters in their reproductive organs, such as reductions of floral parts, uni-ovulate carpels, ortho-campylotropous ovules, dermal integuments, large embryos and absence of endosperm in the mature seed, non-differentiated seed coats and non-dehiscent fruits. The family can be considered to be a relatively specialised and derived one.

According to POSLUSZNY & SATTLER (1973, 1974) the floral apex of *Potamogeton densus* and *P. richardsonii* has a two-layered tunica and the initiation of the carpel primordia is primarily due to periclinal cell divisions in the second tunica layer. This layer should also be responsible for the ovule initiation. These findings seem to be at variance with the three-zonated structure of the ovule primordium as described in this paper. In the case of *Potamogeton*, the carpel and ovule initiation are very difficult to separate. The two processes are continuous since the ovule directly develops out of the adaxial part of the carpel primordium. This discrepancy may be explained by the phenomenon that after the initiation of a carpel by periclinal divisions in the second tunica layer, a "secondarily" three-zonated structure is re-established in the placental region or in the young ovule primordium. Ovules initiated in the second layer, but secondarily becoming three-zonated (and crassinucellate) again are now known from Marantaceae, Droseraceae and Begoniaceae (BOESEWINKEL & DE LANGE 1983). On the other hand, Posluszny and Sattler's drawings and photographs of sections illustrating carpel initiation are not convincing, because they also show anthers and tepals. Since carpels alternate with anthers and tepals, they can not be seen simultaneously in the same median section. A re-examination of carpel and ovule initiation in *Potamogeton* appeared to be necessary to solve this problem.

The two- or three-layered integuments of *Potamogeton* are initiated by periclinal or oblique divisions in two or three neighbouring, dermal initials and sub-

sequently develop by intercalary growth of all participant cells. No specific apical growth could be demonstrated. This type of histogenesis is also described in dermal integuments of many other angiosperms (BOUMAN 1984), but disagrees with the description of ROTH (1957) of *Capsella bursa-pastoris*, where both integuments are said to grow by means of a rim of apical initials exhibiting a bifacial rhythm of cell division.

In *Potamogeton* the ovule and seed fully fill the carpel locule, leaving almost no space between the outer integument and the endocarp. The shape of ovule and seed is the result of a harmonious growth of ovule and fruit. The campylotropous curvature is brought about by the proliferation of mesocarp tissue at the adaxial side of the carpel wall. This proliferation may be compared with the so-called basal body found in many other campylotropous ovules. In *Potamogeton* the basal body is present in the form of a ridge, has no share in the ovule or seed proper, remains attached to the fruit wall and differentiates like the other parts of the endo- and mesocarp. The type of campylotropous curvature of the ovule in *Potamogeton* seems unique and has so far not been found in any other seed plant. Its special nature was recognized as early as 1839 by SCHLEIDEN, who placed the ovule in the new campylotropous type. SCHACHT (1850) rectified Schleiden's description of the ovule and stated that it should be placed in Schleiden's lycotropous type. According to the present study the ovule of *Potamogeton* can be best classified as ortho-campylotropous. The record of campylotropy in the related genus *Ruppia* (Ruppiaceae) needs confirmation.

Ovules with curved embryo sacs, resulting in seeds with curved embryos, are met in many families and at diverse places in the angiosperm system. These ovules and seeds are mostly denominated as campylotropous or amphitropous, terms introduced by MIRBEL (1829) already. Both terms have been re-defined by several authors, often in conflicting ways. This has caused much confusion in the application of the terminology. Several families have been characterized as campylotropous in a part of the literature, and as amphitropous by other authors, and other families as partly campylotropous, partly amphitropous. BOCQUET (1959) and BOCQUET & BERSIER (1960) clearly demonstrated the diversity in the shape of ovules with curved embryo sacs. They showed that campylotropy and amphitropy are independent processes with respect to anatropy. Combining the basic series of ortho-, hemi-, and anatropy with campylotropy and amphitropy, they distinguished nine different types of ovules with curved embryo sacs. These authors also re-defined the amphitropous ovule. Amphitropy must be preceded by a campylotropous phase and be characterized by the formation of a so-called "basal body", which extends into the arch of the nucellus. Indeed, in many ovules such a basal body is present. However, it can be of different ontogenetic origin. It can be formed by the nucellus, the inner integument, the raphe or by two or all in combination. Also the structure of campylotropous ovules without a distinct basal body is diverse. Many ontogenetic processes may be involved in different combinations and to various degrees. Moreover, a curved embryo sac may also develop secondarily from a straight nucellus as a result of the resorbing activity of embryo sac or endosperm. The great diversity

in the distribution and structure of campylotropous ovules renders it plausible that campylotropy has developed more than once, and along several developmental pathways during the evolution of the angiosperms (BOUMAN 1984).

Very little attention has been paid in the pertaining literature to the functional aspects of the different ovule types. The anatropous ovule, of so common occurrence among the flowering plants, is related with angiospermy (or better angioody). In the mainly orthotropous ovules of gymnosperms the pollen can reach the micropyle directly, mostly by becoming affixed to the micropylar droplet. In angiosperms pollen is caught by the stigmas and the ovules have to be reached by pollen tubes growing along the inside of the carpel (stylar) walls. By the anatropous curvature the micropyle has been brought near the base of the ovule, so that anatropy shortens the way for the pollen tube and facilitates the seeking of the right route. In angiosperms orthotropy is correlated mostly with monovuly. It is mostly found in families with a single erect ovule directed towards or even touching the stylar tissue. As regards fertilisation, most campylotropous ovules behave as anatropous ones in having the micropyle near the funicle. *Potamogeton* is one of the few exceptions in this respect. The evolutionary advantage of campylotropy becomes manifest at later stages of development. Campylotropous seeds can contain embryos up to twice as long as the seed itself or even longer, so that campylotropy is a way to longer embryos without much consequences for the length and, so, for the dispersal potential of the seeds. Long embryos have longer roots, hypocotyls and/or cotyledons, and are supposed to have better possibilities in seedling establishment. It is evident that the majority or perhaps all campylotropous seeds have long embryos reaching from micropyle to chalaza.

According to the present authors the existing terms do not reflect adequately the diversity in ontogeny and shape of the ovules and seeds with curved embryo sacs. To classify the existing diversity in campylotropy an extensive terminology is required, which cannot become established without detailed developmental studies. For practical reasons it seems advisable to apply the term campylotropy, with the facultative prefixes ana-, hemi-, or ortho-, for all ovules and seeds with curved embryo sacs. This may prevent further confusion until our insight in the different ontogenetic processes involved and the functional consequences of campylotropy has been extended satisfactorily.

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