Acta Bot. Neerl. 29 (1), February 1980, p. 17–32.

DEVELOPMENT OF OVULE AND TESTA OF LINUM USITATISSIMUM L.

F. D. BOESEWINKEL

Hugo de Vries-laboratorium, Universiteit van Amsterdam, Plantage Middenlaan 2A, 1018 DD Amsterdam

SUMMARY

The ovule primordium of *Linum usitatissimum* is trizonate and both the outer and inner integument are of dermal derivation. The inner integument ultimately becomes about 14 cell layers thick, the inner layer is developed as an endothelium, and the middle layers bring about the ultimate shape of the ripe seed.

The seed-coat is formed out of the outer integument and the outer and inner layers of the inner integument.

The outer layer of the seed-coat consists of slime cells. In an aqueous medium slime diffuses from this layer through ruptures in the cuticle and forms a coat around the seed. The mechanical layers of the seed-coat consist of the fibrous cells of the exotegmen and of the cells of the endotegmen, which latter contain pigment and have pitted walls. The family of the Linaceae is assumed to be related to Geraniaceae, Oxalidaceae or Malpighiaceae.

1. INTRODUCTION

The family of the Linaceae is chiefly tropical in its distribution and contains mostly woody representatives (WINKLER 1931). According to NETOLITZKY (1926), DAVIS (1966) and CORNER (1976) the linaceous ovules are anatropous, bitegmic and crassi- or tenuinucellate.

The genus *Linum* is predominantly suffruticose and more specialised than most of the other genera. The ovules of the cultivated flax have a massive, multicellular archespore and are variable as regards the presence of primary parietal cells (GÉVAUDAN 1959; DAVIS 1966). According to Gévaudan the developing nucellus gives a somewhat chaotic impression because most archesporal cells have a retarded growth and become compressed. Only one of these cells attains full development to form the embryo sac. On account of the economic importance of linseed most of the numerous publications on the seed anatomy of *Linum usitatissimum* are found in pharmacological and agricultural journals and manuals (see, *e.g.*, FLÜCKIGER 1867, TSCHIRCH & OESTERLE 1900, MEYER 1901, MOELLER & GRIEBEL 1928, WIESNER 1928, GASSNER 1931, HAYWARD 1938).

Both integuments partake in the formation of the seed-coat but the most conspicuous layer is the outer layer of slime cells. According to older workers (such as SCHLEIDEN 1857) the epidermal cells contain a mucilaginous substance, but KÜTZING 1851 believed that the slime-forming matter is found on the outer surface of the cell wall of the epidermal cells and becomes suspended in water by boiling or by shaking in cold water. CRAMER (1855) was the first to describe the origin of the slime from the secondary thickening layers of the outer epidermal

cell wall, which observation was confirmed by FRANK (1866/67). According to HABERLANDT (1918) the slime functions principally as a water reservoir, but later a different explanation was given of its main function, *viz.*, the attachment of the seed to the soil in a moist place so that in arid regions the chance of producing offspring becomes greater (MURBECK 1919 and GRUBERT 1974). Details of the composition of the linseed mucilage were given by MANGIN (1893), ANDERSON & LÖWE (1947), ERSKINE & JONES (1957), HIRST & JONES (1958). The mechanical layers of the seed are formed out of the outer layer of the inner integument, which ultimately consists of (in relation to the seed axis) longitudinally oriented fibrous elements, and out of the innermost layer of this integument which is ultimately built up of more or less thick-walled pigment cells.

2. MATERIALS AND METHODS

The material of *Linum usitatissimum* L., *L. perenne* L., *L. narbonense* L., *L. flavum* L. and *L. grandiflorum* Desf. was collected in the Botanical Garden (Hortus Botanicus) of the University of Amsterdam. Fixation took place in Craf and Allen-Bouin mixtures. Sections were made by means of standard microtome techniques. Mature seed-coats were embedded both in paraffin wax and in epon. The following specific strains were used: phloroglucinol – HCl, Sudan IV, ruthenium red and IKI.

The SEM studies were carried out with a Cambridge Stereoscan Mark 2a after a gold-palladium sputtering treatment for 3 min. The treatment of intact seeds consisted of a shorter or longer immersion in water or in 10 % HNO_3.

For the observation of the internal structure of the seed and seed-coat intact seeds were cut through or fragmentation was applied; certain layers could be stripped off or rubbed away to expose the underlying structure. In addition, free hand sections of treated and subsequently air-dried seeds were studied by means of light microscopy in absolute ethanol (to prevent swelling of the mucilaginous layer, so that the structural features of the cell walls could be better observed).

3. RESULTS

Linum usitatissimum has a pentamerous pistil with in each ovary chamber two adjacent ovules which are sometimes abortive. The fruit is a capsule.

3.1. Ovule ontogenesis

The ovule promordia develop from small protuberances on either side of the gynoecial septa. The primordia are trizonate and consist of a corpus (1_3 in *fig. 1* A) surrounded by the initially only anticlinally dividing layers of the subdermatogen (1_2) and dermatogen (1_1). The subdermal archespore is pluricellular and its cells are fairly large and somewhat rich in cytoplasm. In some of the ovules parietal cells can be discerned (*fig. 1* A, C). The nucellus remains fairly small and is completely built up by the archespore, the cells of the subdermal layer, and the epidermis whose apical cells already start dividing periclinally at

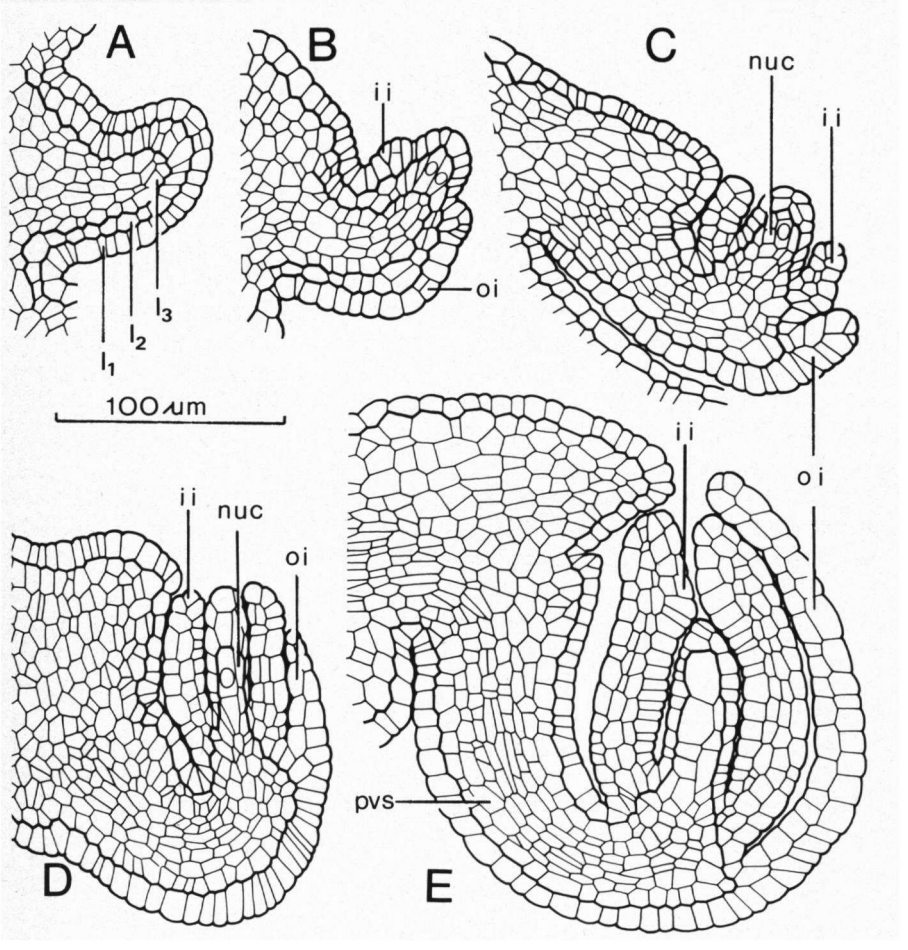

Fig. 1. l.s. of developing ovules of *Linum usitatissimum*. 1_1, 1_2 and 1_3: dermal layer, subdermal layer and corpus, respectively.
es = embryo sac; en = endothelium; end = endosperm; nuc = nucellus; ii = inner integument; oi = outer integument; pvs = provascular strand; ob = obturator; cot = cotyledon.

an early stage of development (*fig. 1* A-E). In more advanced stages no parietal cells can be distinguished any longer. At the stages corresponding with those shown in *fig. 1* D and E the vestiges of the degenerated sporogenous tissue can still be recognised. Finally, the embryo sac (es) is formed in the nucellus top (*figs. 1* E, *2*).The tetrade is linear and the e.s. is formed by the megaspore at the chalazal end (GÉVAUDAN 1959). Already before integument initiation the anatropous curving commences (*fig. 1* A). The inner integument (ii) originates as a complete ring wall by periclinal and oblique divisions in 2 or 3 dermal cells (see *fig. 1* B) and primarily starts growing as a 2-layered structure but fairly soon becomes 3-layered by periclinal divisions in its inner layer (*fig. 1* D). Soon after

the beginning of these periclinal divisions, periclinal divisions of the middle cell layer occur repeatedly throughout the developing i.i. (*fig. 1* E) so that the i.i. ultimately becomes very thick (*figs. 3*A, 2). *Fig. 1* E already shows the radial stretching of the cytoplasm-rich cells of the innermost layer of the i.i. which later form the endothelium.

The outer integument (o.i.) originates shortly after the i.i., also by the division of about three dermal cells en grows out into a two-layered structure (*fig. 1* B-E). Due to the arrested development of the young o.i. cells at the raphal side later only a vague indication of the presence of the o.i. can be discerned in the form of a small dermal cap, so that the ring wall is initially incomplete and in later developmental stages remains markedly asymmetrical. The o.i. becomes locally more than two cells thick only after fertilisation has taken place by periclinal divisions in the inner cell layer on either edge of the ovule.

3.2. the full-grown ovule

The fully developed ovule is anatropous, bitegmic and crassinucellate (*fig. 2*). The nucellus is slender and longitudinally elongate; at this stage the enlarged e s has already resorbed the nucellar apex. According to DAVIS (1966) the e.s. is of the *Polygonum* type.

At the inner side of the cytoplasm-rich endothelium a structure resembling a cuticle is present. In the basal part of the nucellus sometimes an only partly developed sporogenous cell is found (*fig. 2*) which cell represents a remnant of the originally pluricellular archespore. The i.i. is about 12 cell layers thick at the most. The micropyle is formed by the i.i. as a narrow channel somewhat compressed in the funicular plane. The obturator, which connects the stylar canal and the micropyle, is covered with cytoplasm-rich dermal cells developed as trichomes. The ovules of *Linum flavum* and *L. narbonense* resemble those of *L. usitatissimum* very closely.

3.3. Development of seed and seed-coat

The endosperm is initially nuclear and is situated peripherically in the e.s. Cell wall formation proceeds centripetally and becomes complete. According to DAVIS (1966) the endosperm is of the helobial type.

The lower part of the e.s. gradually becomes separated from the remainder as the result of a local constriction by the inner integument (BILLINGS 1901, SCHÜRHOFF 1924, VAN WISSELINGH 1919). The detached part of the e.s. originally functions as an endosperm haustorium but after it has become completely severed it ceases to function as such.

The shape of the cells of the inner epidermis of the i.i. gradually changes from radially stretched to tangentially flattened and ultimately they become tanniniferous (*figs. 3*C, D). This cell layer becomes tightly joined to the endosperm after wall formation in the endosperm and the resorption of the middle layers of the i.i. (*fig. 3*D). According to VAN WISSELINGH (1919) and NETOLITZKY (1926) there is a cuticle between endosperm and seed-coat. In the middle layers of the i.i. some divisions take place so that it may in places attain a thickness of up to 14 cell

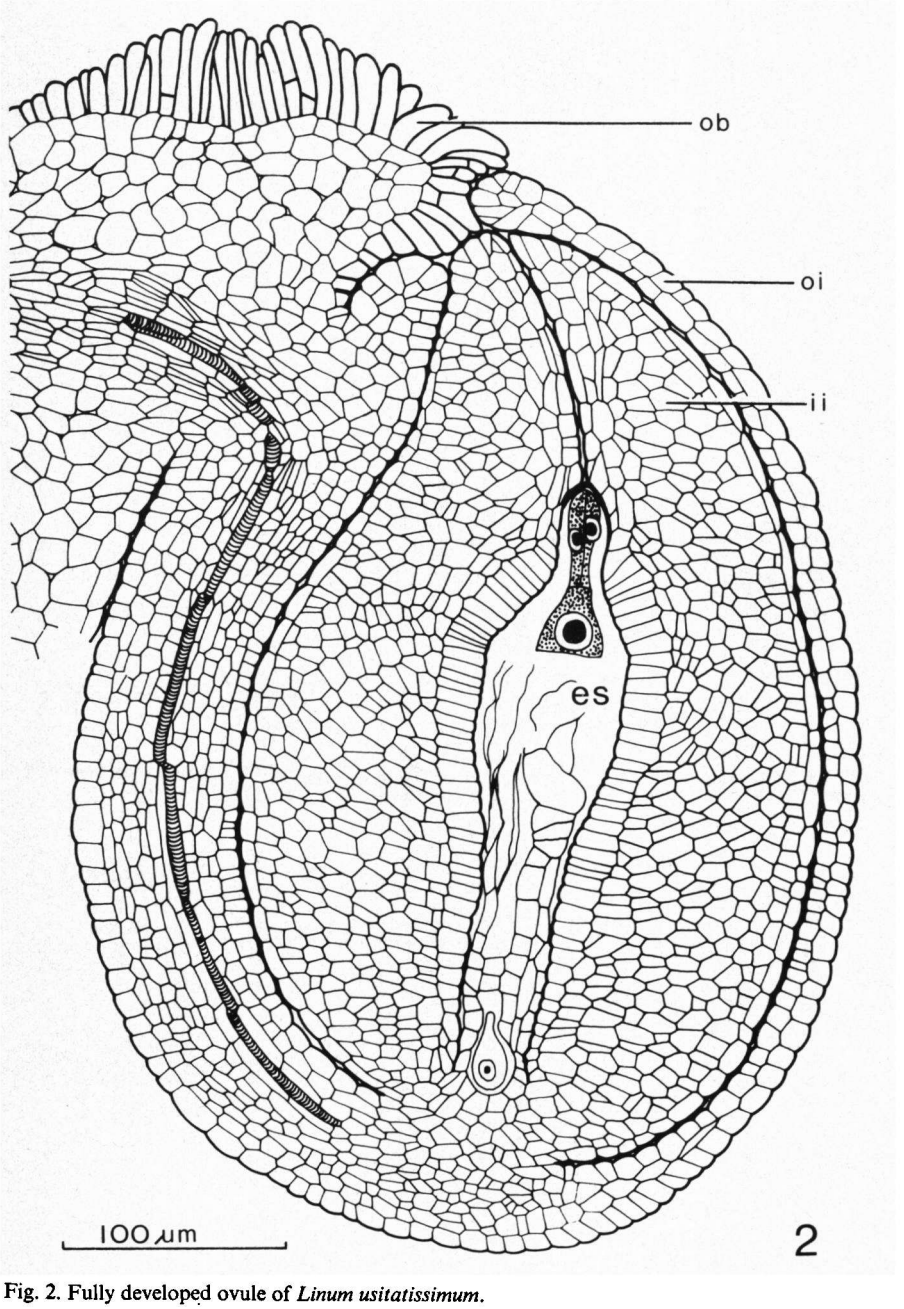

Fig. 2. Fully developed ovule of *Linum usitatissimum*.

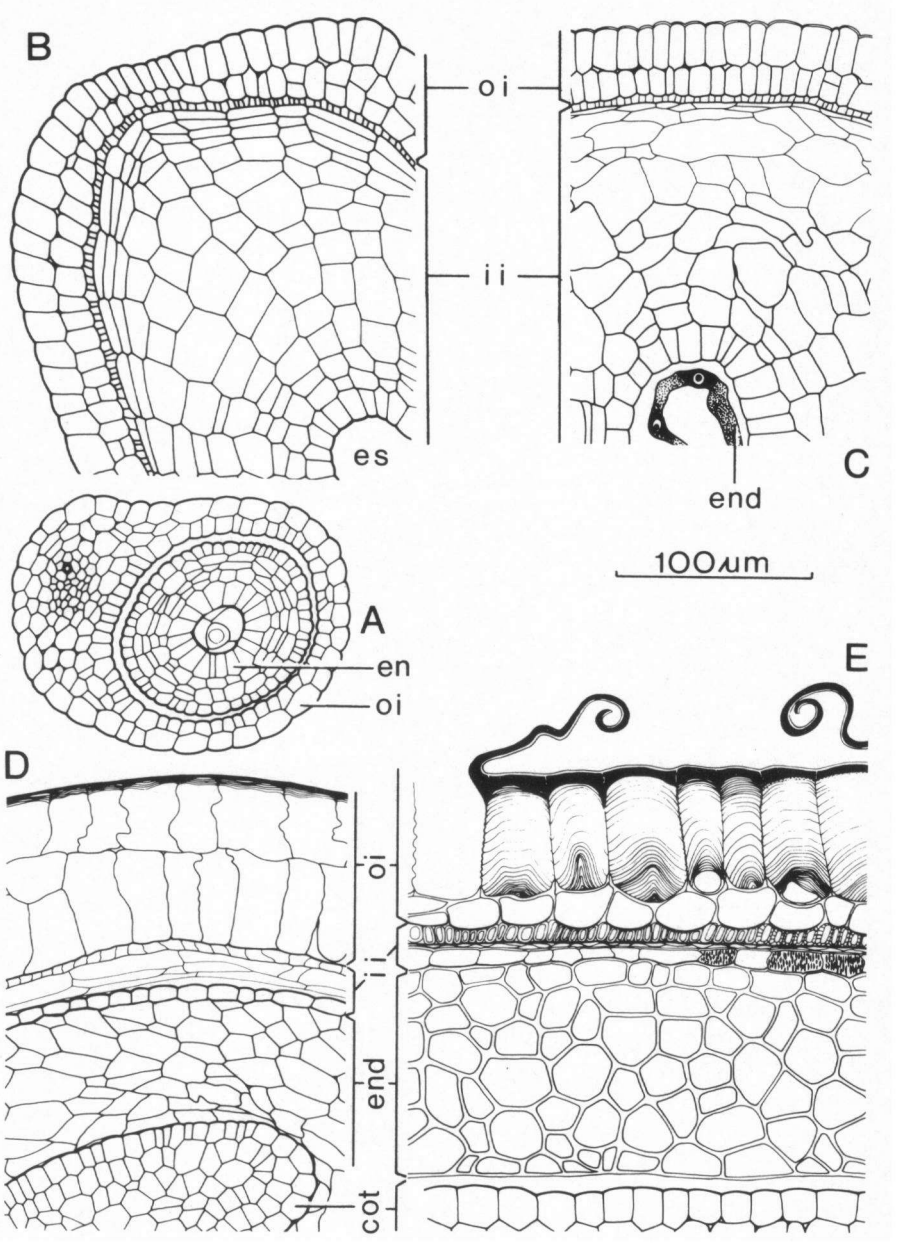

Fig. 3. Ovule (A) and development of seed-coat as seen in cross sections.

layers and at that stage forms the bulk of the volume of the growing seed. This mitotic activity takes place more frequently in the median plane of the seed and the cells also become larger there than in the transversal plane, so that the developing seed becomes flattened (*fig. 3* B). The middle layers of the i.i. are originally rich in starch, but later they stretch to become very large, poor in cytoplasm, and thin-walled, and thus form a tender tissue. The cells adjacent to the endothelium longest remain cytoplasm-rich. The subdermal cells of the i.i. do not enlarge to the same extent as do the other cells and they also stretch in the direction perpendicular to the longitudinal axis of the seed (*fig. 3* B, C); these cells also have thicker walls and are the only ones of the middle i.i. layers of which recognisable remnants are discernible in the mature seed-coat between the sclerenchymatous and pigment layers. The other cells of the middle layers collapse (*fig. 3* D). The nuclei of the cells of the outermost cell layer of the i.i. become more oblong and these cells stretch in the longitudinal direction of the seed whilst following the increase in girth by numerous anticlinal cell divisions (*fig. 3* B, C, D) ultimately to become sclerotic. The o.i. is partly two-layered except alongside the seed edges where it may become about four cells thick by periclinal divisions of the inner cell layer (*fig. 3* B). Of the cells later forming the edge of the seed those of the outer layer do not stretch as much as the other ones and those of the innermost layer only scarcely so. All cells of the o.i. enlarge to a considerable extent during seed development and become rich in amyloplasts. On the outer surface of the o.i. a manifest cuticular layer is formed. Immediately before full maturity is attained the first slime-forming layers are deposited (*fig. 3* D). During the formation of these thickening layers the cells still contain numerous amyloplasts but by the time the thickening reaches its maximum all starch grains have disappeared; they are presumably metabolised when the slime-producing substance is deposited.

3.4. The mature seed

The mature seed-coat is formed by the whole of the o.i. and by the outer- and innermost layers of the i.i. The most conspicuous seed-coat layer is the outermost slime-producing one which is covered with a rugose-plicate cuticule poor in cutin (*figs. 3*E, *4*C, D, E). The shape of the mucilage cells is not the same throughout: along the edge of the seed the cells are elongate (*fig. 4* C) whereas they are polygonal in the other parts of the seed coat (*fig. 4* D). The mucilaginous wall layers exhibit a positive reaction with ruthenium red, but the first-formed wall layers immediately below the cuticle stain even more strongly. When hand sections of linseed are microscopically observed in the dry state or in absolute alcohol the mucilage-forming cells appear as a structureless, opaque layer. When a little water is gradually added to the alcohol the slime cells swell to some extent, so that the individual thickening layers and separating walls become visible. In most of the cells a lumen is hardly discernible. Addition of water to dry sections causes a sudden and considerable swelling of these cells in a radial direction by which the cells may stretch to twice or three times their original length. The radial cell walls become passively stretched, which is facilitated by the presence of

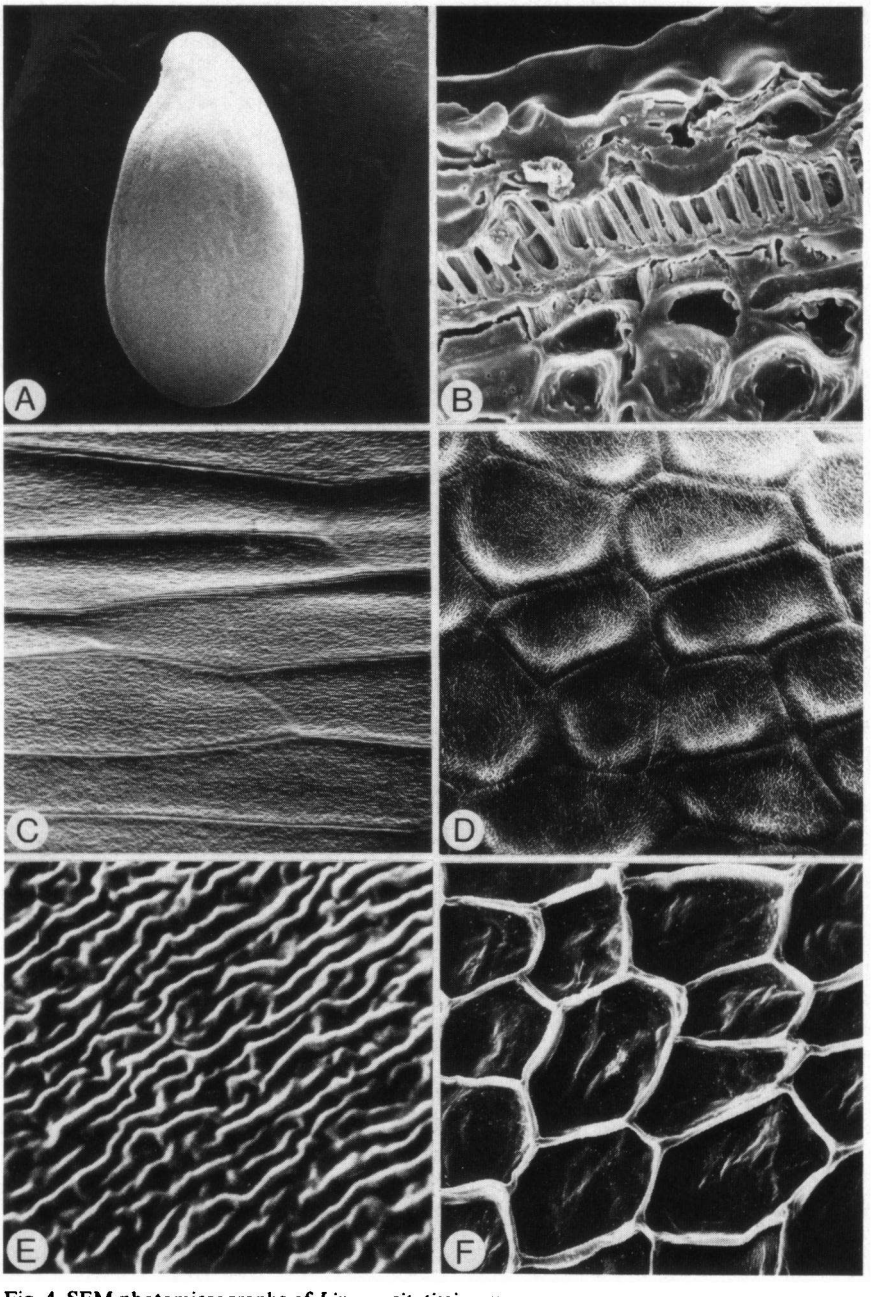

Fig. 4. SEM photomicrographs of *Linum usitatissimum*.
A: seed. (magnif. about × 10);
B: t.s. of seed-coat (× 500);
C,D: seed-coat as seen from above in the raphal (× 1000) and in the micropylar region (× 5000);
E: detail of cuticular structure (× 5000);
F: seed-coat after a 16 hrs. treatment with HNO_3. Cuticle and outer wall have disappeared (× 500).

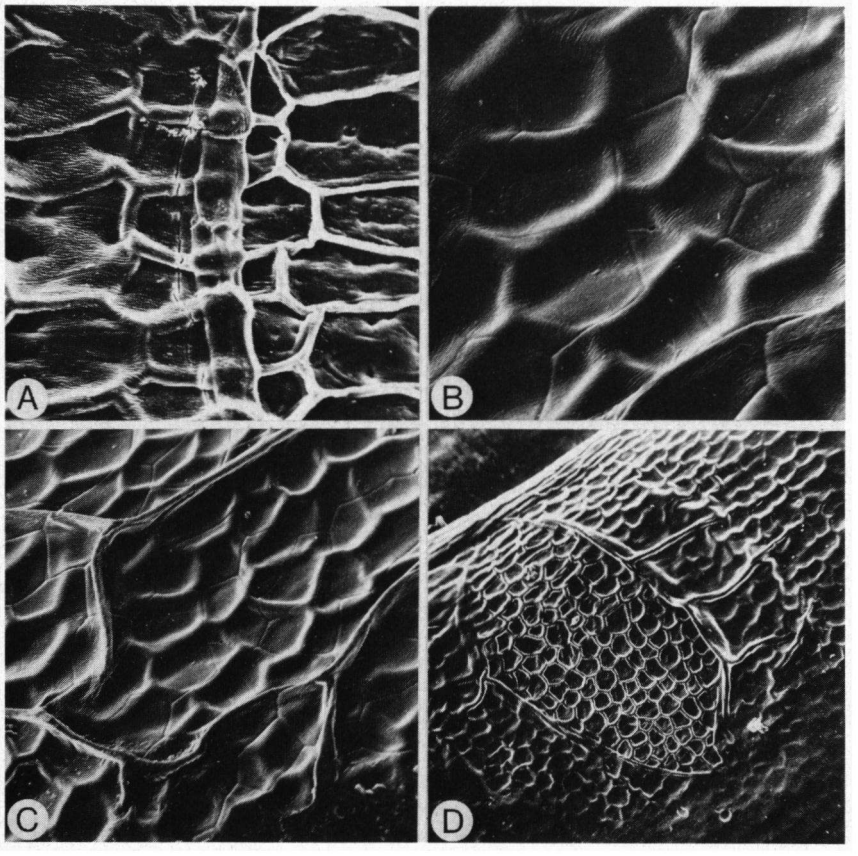

Fig. 5. SEM photomicrographs of *Linum usitatissimum*
A, B, C: photomicrographs of the seed-coat after a 16 hrs. treatment with HNO_3.
A: cuticle partly removed (magn. about × 250);
B: shifted cuticle (× 250);
C: pleated cuticle (× 125);
D: seed-coat after a $2\frac{1}{2}$ days sojourn in water with forming protruding folds in parts (magn. about × 40).

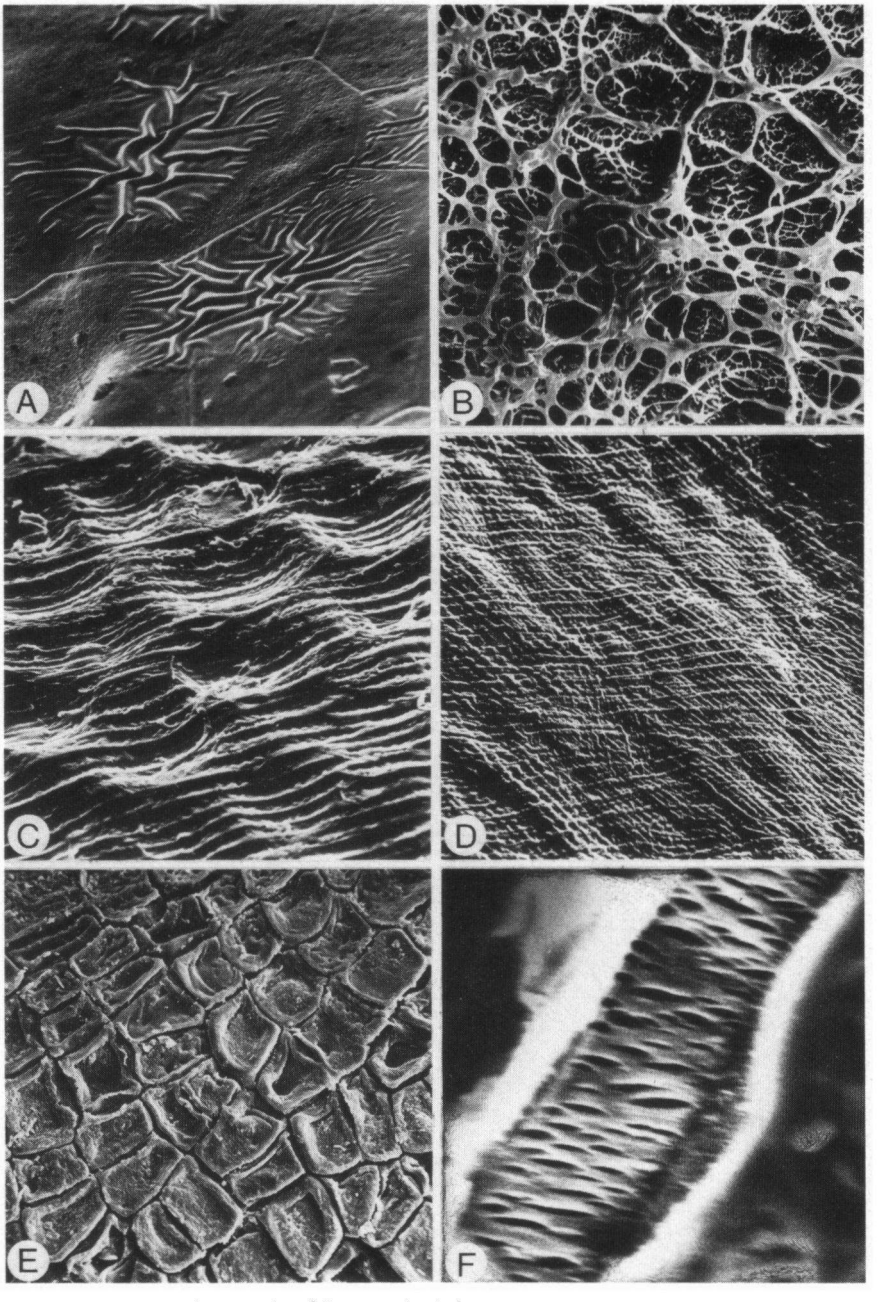

Fig. 6. SEM photomicrographs of *Linum usitatissimum*
A: seed-coat after 16 hrs. in H_2O–cells intact (magn. about × 1000);
B: dried mucilage on seed-coat (× 500);
C: sclerotic layer of seed-coat after removal of o.i. (× 500);
D: sclerotic layer seen from the inside (× 250);
E: pigment layer seen from above (× 500);
F: anticlinal wall of pigment cell with pits (× 2500).

numerous, minute folds in these walls which become almost completely smoothed out (*fig. 3* E). The folds presumably originated when the originally water-rich slime-cells desiccated during seed maturation. The strong and sudden swelling of the slime-cells causes ruptures in the cuticle, which usually remains connected with the peripheral cell wall layer in many places, so that they sometimes curl up together. Observation of whole seeds soaked in water for several hours under a stereo-microscope shows that the cuticle is lifted or torn in a number of places, especially near the sharp edge of the seed. The slime exudes only through the ruptures in such a way that the original cell pattern is still recognisable. When seeds have been soaking in water long enough germination is initiated by the splitting of the seed coat along the sharp edge of the seed in the micropylar area. The pigment layer (which does not tightly adhere to the other parts of the seed coat) protrudes from the slit and later the rootlet appears.

SEM observation of the seed coat of whole seeds pretreated for about 16 hrs in water or 10% nitric acid reveals that their cuticles are often finely wrinkled and torn (*figs. 5* A-D, *6*A). Especially the treatment with HNO_3 causes the cuticle to become fully detached from the rest of the seed by the rupturing of the anticlinal epidermal cell walls. This is usually concomitant with wrinkling, so that the original cell pattern becomes obliterated, especially when the cuticle has also shifted. After the cuticle and the peripheral parts of the cell walls have disappeared, the basal, suberised cell walls come directly into view. Free hand sections of such seeds after a sojourn in water for about 16 hrs. contain all of the slime producing substance in the intact cells which retain their swelling capacity (*fig. 5* A). Seeds treated with diluted nitric acid have lost their mucilage completely. Slime diffused out of the outer cell layer and subsequently dried may have a ropy appearance, which may be expected on account of its great adhesive power.

The seed-coat as a whole consists of five well-distinguishable layers *viz.* (*fig. 3* E):

1. The outer layer of mucilage cells, whose slime-forming substance is well screened from the remainder of the seed by the basal, suberised cell wall parts.
2. The innermost layer of somewhat flattened cells of the o.i., whose cells are often referred to by the name of "ring cells" owing to their suborbicular outline in surface view.
3. The outermost layer of the i.i. consisting of thick-walled, lignified cells oriented as fibrous elements in the longitudinal direction of the seed (*fig. 6* C). Between the fibres there are numerous, often somewhat longitudinally extended pits which give the inner surface of the cell wall a grooved appearance (*figs. 3* E, *4* B). The tangential cell walls are thinner than the lateral ones. The peripheral ring cells protrude into the sclerenchymatous layer so that the latter has an undulate appearance when seen in surface view (*fig. 6* C); the protrusions are also clearly discernible in transverse sections (*figs. 3* E, *4* B). Along the narrow edge of the seed the sclerenchymatous elements are relatively larger and more thick-walled, and the protrusions are more elongate.
4. The almost completely compressed and partly resorbed remains of the cell layers situated immediately below the sclerenchyma layer. These appear as a

striation crossing the fibrous elements almost perpendicularly and have for that reason been dubbed "*Querzellen*" (cross-cells); see *fig. 6* D.

5. The innermost layer of the i.i. known as the pigment layer and consisting of somewhat tangentially elongate cells completely filled with tannic substances (*fig. 6* E). The cell walls are somewhat thickened and the anticlinal walls contain elongate pits (*figs. 3* E, *6* F). When the pigment layer is seen in surface view under the light microscope these pits look saw-edged. The pigment layer is tightly connected with the oleaginous endosperm.

The endosperm becomes thinner towards the sharp edges of the seed. The oleiferous and but little starch-containing embryo is fairly large and straight. The cotyledons lie in the median plane. The raphal bundle is amphicribral and is degenerated in the fully mature seed. According to NETOLITZKY (1926), there is no corky plugging of the chalaza.

The seed is laterally much flattened, 4 × 2 × 1 mm, of a shiny brown color, and faintly pitted; the pigment layer is responsible for the brown coloration of the testa.

The seed-coats of other *Linum* species as far as seen do not differ much of that of *Linum usitatissimum*.

4. DISCUSSION

The ovule of *Linum usitatissimum* has a slender nucellus and is variable as regards the presence of parietal cells. According to RAO (1968) and NARAYANA (1970) there is a tendency within the family of the Linaceae towards a progressive reduction of the nucellar tissue, which trend even leads to a tenuinucellare condition in the herbaceous representatives. Also in *Anisadenia saxatilis* ovules with and without parietal cells are found (RAO 1968), and *Linum perenne* (RAO) and *Radiola linoides* (MAURITZON 1934) are even completely tenuinucellate. According to CORNER (1976) the i.i. of the Linaceae may be from 3 to 12 cell layers thick. Since it tends to be thicker in the herbaceous forms (see also CRETÉ 1937) it is thought to be a derived condition. Corner also reports that in the Linaceae the o.i. is only 2–3 layers of cells thick and that any enlargement is brought about by divisions of the innermost layer alone. According to Rao the o.i. is two-layered in 7 out of the 9 representatives studied by him and 3-layered in the other two. The obvious corollary is that in this family the o.i. is consistently of dermal derivation. The endothelium and obturator are according to Rao a constant familial characteristic. A pluricellular archespore occurs also in *Anisadenia* and *Hugonia* (RAO) and in *Radiola linoides* (MAURITZON).

The presence of tenuinucellate ovules and a solid i.i. are additional arguments pleading in favour of an advanced status of the genus *Linum*. The same conclusion was arrived at by HEIMSCH & TSCHABOLD (1972) on anatomical grounds, although they believe that several species of *Linum* have retained some primitive characters. BRANDZA (1891) described the ovule of *Linum* as unitegmic. He mistook the i.i. for the nucellus and erroneously concluded that the pigment layer

is of nucellar origin (see also GUIGNARD 1893). This error was repeated in MCLEAN & IVIMEY-COOK (1964, p. 1484). Within the Linaceae the endosperm is predominantly nuclear (RAO), but in the cultivated flax and in some other species of *Linum* the helobial type of endosperm formation has been recorded. In addition, in these species, the basal part of the e.s. is gradually severed from the remainder after it has functioned as a haustorium (BILLINGS 1901, VAN WISSELINGH 1919, SCHÜRHOFF 1924). According to DORASAMI & GOPINATH (1945) *Linum mysorense* does not have a helobial endosperm, but the basal endosperm haustorium is gradually cut off as in the other species studied.

Owing to the economic importance of linseed the seed-coat anatomy and more particularly the epidermal layer of mucilage cells has been studied frequently, as mentioned before, from an agricultural and pharmacological point of view (HOFMEISTER 1854, CRAMER 1855, FRANK 1866–1867, NOBBE 1876, COLLIN & PERROT 1904). Most workers are of the opinion that when the seeds are immersed in water and swell, the slimy substance protrudes through rents in the burst cuticle. A smaller number (HOFMEISTER 1854, SEMPOLOWSKI 1874a, b, KOBUS 1884) has maintained that the mucilage moves through the intact cuticle (through interstitial cavities between the molecules). In either case water will have to penetrate through the cuticle to the slime-forming layer before any swelling can occur.

The present study confirms the opinion that the slime protrudes through lesions in the cuticle.

Seeds treated for 16 h with 10% nitric acid do not retain any mucilage; the slime is apparently dissolved or has been chemically transformed into more soluble substances. ANDERSON & LÖWE (1947) also found a decrease of viscosity after boiling of linseed in diluted HCl, so that the solution readily passes through filter paper.

Most workers believe that the cuticle is impermeable to the mucilage, so that the pressure built up by the swelling slime layer leads to rupturing so that the slime can escape (FLÜCKIGER 1867, MANGIN 1893, KORAN 1899, TUNMANN 1913, HABERLANDT 1918, WIESNER 1927, HAYWARD 1938).

According to KORAN (1899) the tears form both over the anticlinal cell walls and elsewhere in the outer wall. He suggested a preformation of zones of rupturing in the form of slime pores in the wall, but such perforations have never been observed and simply do not exist. MANGIN (1893) already pointed out that the cuticle covering the slime cells does not contain interstitial cavities or perforations and that even if they were present the cuticle would tear apart anyway. HAYWARD (1938) cites HABERLANDT (1918) who explained that the increasing pressure exerted on the outer wall causes the rupturing of the not very elastic anticlinal walls so that the raised outer walls must burst. All workers mentioning cuticular rupturing studied hand sections without realising that the tension relations in the sections of the cuticle may be altogether different from those in cuticles of whole seed – one may expect to find more torn places in sectioned material.

The conclusion may be drawn that the cuticle is impermeable to slime and

somewhat elastic. The pressure of the swelling mucilage layers causes the rupturing of anticlinal cell walls in the epidermis, so that the cuticle is lifted off in many places and may also become torn, which enables the slime to protrude from the mucilage cells.

A comparison of this mechanism with conditions in the related Oxalidaceae (BOUMAN 1974) reveals that in some species of *Oxalis* the cuticle causes a ballistic dispersal of the seed minus its cuticle and part of the o.i. Within the family of the Linaceae slime epidermides are not common; they have also been recorded from *Reinwardtia*, *Hesperolinon* and *Radiola* (WINKLER 1931; CORNER 1976). In this family the outer layer of the i.i. develops into the exotegmen of the seed-coat, and its inner layer at first forms an endothelium which later becomes the pigment layer (CORNER 1976, RAO 1968). The seed-coat anatomy of *Hugonia* (placed in a separate family of the Hugoniaceae by some authors) differs to some extent from that of the other genera of the Linaceae: the exotegmen becomes sclerotic in the micropylar area only, the testa is fairly thick and its meso- and endotesta cells are partly sclerotised. Corner states: "*The simple tegmen of Lineae may, therefore, be reduced from a mesotestal construction represented by Hugonieae*".

It is fairly generally accepted that Linaceae, Oxalidaceae and Geraniaceae are closely related families (ENGLER 1964 and others). According to WINKLER (1931) the Linaceae constitute an "old" family with a nowadays disintegrated area of distribution reduced to isolated patches. NETOLITZKY (1926) has shown that it is possible to derive the testa of *Linum* from that of the Geraniaceae. HOEFFGEN (1922) found a close serological affinity between the three above-mentioned families. The similar ovular ontogeny in these families also suggests their great taxonomic affinity (compare BOUMAN 1974, BOESEWINKEL 1979): both the o.i. and i.i. are of dermal derivation and in early phases of development two cell layers thick, the i.i. becoming 3-layered at a somewhat later stage by periclinal divisions in the inner cell layer to be followed later by periclinal divisions in the middle layer thus formed (in Geraniaceae only in some places); and the o.i. may become thicker by divisions in the inner cell layer.

CORNER (1976), basing his conclusions on the seed-coat structure, pointed out that both Linaceae and Celastraceae have a fibrous exotegmen. He is of the opinion that Linaceae and Geraniaceae are not so closely related because in the latter family the seeds do not have an exotegmen consisting of fibrous elements but of more or less star-shaped cells. He accepts manifest relationships between Linaceae, Malpighiaceae, and possibly Oxalidaceae. According to HALLIER (1923) the Linaceae are the centre from which a large number of families have developed in many directions. FROHNE & JENSEN (1979) are of the opinion that the families usually united in the Rutales-Geraniales complex are not necessarily related. As far as the place of the Linaceae is concerned, one must bear in mind that the ontogeny of the ovule and the seed-coat anatomy is chiefly known from *Linum* and *Radiola* and that our knowledge is thus too limited to permit more definite conclusions. A broader knowledge of these features, especially of the tropical genera, is urgently required.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. F. Bouman for useful discussions and Professor A. D. J. Meeuse for his interest, encouragement and critical translation of the original Dutch draft. The technical assistance of mr. J. Geenen is gratefully acknowledged.

REFERENCES

ANDERSON, E. & H. LÖWE (1947): The composition of flaxseed mucilage. *J. Biol. Chem.* **168:** 289–297.

BILLINGS, F. H. (1901): Beiträge zur Kenntnis der Samenentwicklung. *Flora* **88:** 253–318.

BOUMAN, F. (1974): *Developmental studies of the ovule, integuments and seed in some Angiosperms.* Thesis, University of Amsterdam. Naarden.

BOESEWINKEL, F. D. & W. BEEN (1979): Development of ovule and testa of Geranium pratense L. and some other representatives of the Geraniaceae. *Acta Bot. Neerl.* **28:** 335–348.

BRANDZA, M. (1891): Développement des téguments de la graine. *Rev. Gén. Bot.* **3:** 227–240.

COLLIN, E. & E. PERROT (1904): *Les résidus industriels utilisés par l'agriculture.* Paris.

CORNER, E. J. H. (1976): *The seeds of dicotyledons* (2 vols.) Cambridge.

CRAMER, C. (1855): Über das Vorkommen und die Entstehung einiger Pflanzenschleime. Bau und Entwicklungsgeschichte der Leinsamen. In: C. NÄGELI & C. CRAMER: *Pflanzenphysiologische Unters.* **III:** 1–9. Zürich.

CRETÉ, P. (1937): Développement et structure du tégument séminal chez le Radiola linoïdes Roth. *Bull. Soc. Bot. Fr.* **84:** 655–659.

DAVIS, G. L. (1966): *Systematic embryology of the angiosperms. New York, London, Sydney.*

DORASAMI, L. S. & D. M. GOPINATH (1945): An embryological study of Linum mysorense Heyne. *Proc. Indian Acad. Sci.* **B22:** 6–9.

ENGLER, A. (1964): *Syllabus der Pflanzenfamilien II.* Berlin.

ERSKINE, A. J. & J. K. N. JONES (1957): The structure of linseed mucilage. Part I. *Can. J. Chem.* **35:** 1174–1182.

FLÜCKIGER, F. A. (1867): *Lehrbuch der Pharmakognosie des Pflanzenreiches.* Berlin.

FRANK, A. B. (1866–1867): Ueber die anatomische Bedeutung und die Entstehung der vegetabilischen Schleime. *Jahrb. wiss. Bot.* **5:** 161–200.

FROHNE, D. & U. JENSEN (1979): *Systematik des Pflanzenreichs.* Stuttgart-New York. 2.Auflage.

GASSNER, G. (1931): *Mikroskopische Untersuchung pflanzlicher Nahrungs- und Genussmittel.* Jena.

GÉVAUDAN, M. A. (1959): Mégasporogénèse et différenciation du sac embryonaire chez Linum usitatissimum. *Rev. Gén. Bot.* **66:** 53–76.

GRUBERT, M. (1974): Studies on the distribution of myxospermy among seeds and fruits of Angiospermae and its ecological importance. *Acta Biol. Venez.* **8:** 315–551.

GUIGNARD, L. (1893): Note sur l'origine et la structure du tégument séminal chez les Capparidées, Résédacées, Hypericacées, Balsaminées et Linacées. *Bull. Soc. Bot. Fr.* **40:** 56–59.

HABERLANDT, G. (1918): *Physiologische Pflanzenanatomie.* Leipzig.

HALLIER, H. (1923): Beiträge zur Kenntnis der Linaceae (D.C. 1819) Dumort. *Beih. bot. Centrbl.* **39,** 2: 1–178.

HAYWARD, H. E. (1938 sec. ed. 1967): *The structure of economic plants.* New York.

HEIMSCH, C. & E. E. TSCHABOLD (1972): Xylem studies in the Linaceae. *Bot. Gaz.* **133:** 242–253.

HIRST, E. L. & J. K. N. JONES (1958): The gums and mucilages of plants. In: *Handbuch der Pflanzenphysiologie (ed. W. Ruhland)* **IV:** 500–517. Berlin, Göttingen, Heidelberg.

HOEFFGEN, F. (1922): Sero-diagnostische Untersuchungen über die Verwandschaftsverhältnisse innerhalb des Columniferen-Ästes der Dicotylen. *Bot. Arch.* **1:** 81–89.

HOFMEISTER, W. (1854): Über die zu Gallerte aufquellenden Zellen der Aussenfläche von Samen und Perikarpien. *Ber. Verh. d. Königl. Sächsischen Ges. d. Wissenschaften* **8:** 18–37.

KOBUS, J. D. (1884): Kraftfutter und seine Verfälschung. *Landwirtsch. Jahrb.* **13:** 813–850.

KORAN, J. (1899): Der Austritt des Schleimes aus dem Leinsamen. *Pharm. Post* **32:** 221.

KÜTZING, F. T. (1851): *Grundzüge der Philosophischen Botanik* I. Leipzig.

McLEAN, R. C. & W. R. IVIMEY-COOK (1964): *Textbook of theoretical botany* II. London.
MANGIN, L. (1893): Observations sur l'assise à mucilage de la graine de Lin. *Bull. Soc. bot. Fr.* **40:** 119–135.
MAURITZON, J. (1934): Zur Embryologie einiger Gruinales. *Svensk. bot. Tidskr.* **28:** 84–102.
MEYER, A. (1901): *Die Grundlagen und die Methoden für die microskopische Untersuchung von Pflanzenpulvern.* Jena.
MOELLER, J. & C. GRIEBEL (1928): *Mikroskopie der Nahrungs- und Genussmittel aus dem Pflanzenreich* (3 Aufl.). Berlin.
MURBECK, S. (1919): Beiträge zur Biologie der Wüstenpflanzen. I. Vorkommen und Bedeutung v9n Schleimabsonderung aus Samenhüllen. *Lunds Univ. Årsskr. N.F., Avd.* 2, **15** (10): 1–36.
NARAYANA, L. L. (1970): Linaceae, in: *Symposium on comparative Embryology of Angiosperms:* 127–132. Delhi.
NOBBE, F. (1876): *Handbuch der Samenkunde.* Berlin.
NETOLITZKY, F. (1926): Anatomie der Angiospermen-Samen. In: K. LINSBAUER (ed.), *Handbuch der Pflanzenanatomie.* Band **X,** 4. Berlin.
RAO, D. (1968): Contribution to the embryology of Linaceae. *J. Osmania Univ.* (Science) Golden Jubilee number.
SCHLEIDEN, M. J. (1857): *Handbuch der botanischen Pharmacognosie.* Leipzig.
SCHÜRHOFF, P. N. (1924): Zytologische Untersuchungen in der Reihe der Geraniales. *Jahrb. wiss. Bot.* **63:** 707–759.
SEMPOLOWSKI, A. (1874a): Ueber den Bau der Schale landwirtschaftlich wichtiger Samen. *Landwirtsch. Jahrb.* **3:** 823–866.
— (1874b): *Beiträge zur Kenntnis des Baues der Samenschale.* Thesis Leipzig.
TSCHIRCH, A. & O. OESTERLE (1900): *Anatomischer Atlas der Pharmakognosie und Nahrungsmittelkunde.* Leipzig.
TUNMANN, O. (1913): *Pflanzenmikrochemie.* Berlin.
WIESNER, J. VON (1927): *Die Rohstoffe des Pflanzenreichs* 4. Leipzig.
WINKLER, H. (1931): Linaceae, in: ENGLER & PRANTL, *Die natürlichen Pflanzenfamilien* 2. Aufl. **19a:** 82–130. Leipzig.
WISSELINGH, C. VAN (1919): Bijdragen tot de kennis van de zaadhuid. 5. Over de zaadhuid der Linaceën. *Pharm. Weekbl.* **43:** 1437–1448.