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Ovule and seed development in Droseraceae

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SUMMARY

A structural analysis of ovule and seed development in the four genera of the Droseraceae is given. The ovule primordia of the Droseraceae are dizonate. The integuments are dermal in origin. The ovules of *Dionaea, Aldrovanda* and *Drosera* are characterized by nucellar elongation and strongly enlarged cells of the nucellar epidermis. This feature is lacking in *Drosophyllum*. The differences in the seed coat of the four genera are mainly due to variations in the differentiation of the testa. *Drosophyllum* has an endotestal crystal layer, *Dionaea* and *Aldrovanda* are exotestal and exo-/endotestal respectively, whereas *Drosera* has a less complex testa. Contrary to the testa, the tegmen shows more correspondence. It consists of an endotegmic sclerotized or pigment layer and crushed remaining outer tegmic layers. As a consequence, in spite of the variable testa structure the basic seed coat structure is similar in the four genera. In *Drosophyllum, Dionaea* and *Drosera* the sclerotic layers of the seed coat are not lignified. Although the seed dimensions are different, the operculate seeds with starchy endosperm and small embryo have a similar construction. From the point of view of the seed anatomy, the four genera are correctly placed in the Droseraceae.

Key-words: Droseraceae, endotegmen, operculum, seed anatomy.

INTRODUCTION

The family Droseraceae consists of carnivorous herbs and comprises the monotypic genera *Drosophyllum, Dionaea* and *Aldrovanda* and the larger genus *Drosera* with three subgenera and about 85 species.

Drosophyllum, Dionaea and *Aldrovanda* are sharply delimited genera, the first two also with a narrow geographical distribution (Diels 1936; Takahashi & Sohma 1982). *Drosophyllum* is endemic to the western part of the Mediterranean region, *Dionaea*, the Venus fly-trap, is endemic to the South-east of the USA, whereas *Aldrovanda* has a disjunct area, extending from Europe through Central Africa, India and Japan to Australia. The genus *Drosera* is cosmopolitan with the greatest speciation in Australia and New Zealand.

The suffruticose *Drosophyllum* grows on sandy soils under pine trees. The other herbaceous genera occur in bogs and on other waterlogged soils, but *Aldrovanda* is a submerged water-plant (Heywood 1978). These genera show adaptations to their water-rich environment. The most typical character of the Droseraceae is their carnivory. For this purpose the genera have different morphological and anatomical adaptations.

Drosophyllum and *Drosera* resemble each other in their external morphology and trap

mechanism (fly-paper type). Their trap consists of a great number of stalked glands, mainly on the leaves, which exude sticky droplets with digestive enzymes. Contrary to *Drosophyllum*, in *Drosera* the tentacles, and to a certain degree also the leaves, have the ability to envelop the captured prey by performing slow incurving movements.

Dionaea and *Aldrovanda* have two-lobed leafblades which close immediately when an animal gives an appropriate stimulus to the trigger hairs on the leaf surface (active trap).

It is assumed that by digesting small animals the Droseraceae may supplement their low nitrogen or phosphorous supply in their nutritionally poor environments.

The syncarpous ovary is one-loculed and consists of five, four or three carpels fused with their margins. All genera have numerous seeds per fruit, but *Drosera* often has a large amount of dust seeds. The fruit is a loculicidal capsule which does not open in *Aldrovanda*. The placentation is basal or parietal and the ovules are anatropous, bitegmic and either crassinucellate or tenuinucellate in some *Drosera* species, with the micropyle formed by the inner integument (Pace 1912; Netolitzky 1926; Davis 1966; Corner 1976; Favard 1963). Smith (1929) and Teryokhin (1986) studied the embryology and seed coat anatomy of *Dionaea* and *Aldrovanda*. The chalazal megaspore develops into a Polygonum type of embryo sac (Davis 1966; Patankar 1956).

The lateral nucellar cells become radially elongated to form a conspicuous jacket around the embryo sac. The endosperm formation is initially nuclear and the chalazal part has a haustorial function. According to Cronquist (1981) the fleshy and solid endosperm is granular and starchy as well as oily and proteinaceous.

The small embryo is situated below the micropyle and at germination the root pushes a small operculum, formed by the tips of the inner integument, outwards (Netolitzky 1926; Corner 1976). The tips of the cotyledons have a haustorial character and in *Drosophyllum* and *Aldrovanda* the cotyledons remain enclosed within the seed during germination (Diels 1906).

The data on the seed coat structure are scattered in literature. Corners' (1976) review on the family is mainly based on Netolitzky (1926) and gives a misinterpretation of the tegmic layers and nucellar remnants in *Drosophyllum*. Corner's suggestion of a pachychalazal seed in *Dionaea* is also not correct. The genera agree in the presence of an endotegmic, tanniniferous layer and crushed outer tegmic layers.

Drosophyllum has an endotestal crystal layer and a partly sclerotized tegmen (Netolitzky 1926); the seed coat of *Dionaea* is exotestal (Smith 1929); *Aldrovanda* combines an exo- and endotesta (Teryokhin 1986) and *Drosera* has a less complex testa.

Several authors have questioned the placement of *Drosophyllum*, *Dionaea* and *Aldrovanda* in Droseraceae and proposed the separate families Dionaeaceae Dum. and Aldrovandaceae Nak. (See Takakashi & Sohma 1982). In most recent classifications the four genera are placed together in Droseraceae.

The opinions concerning the superfamilial relationships of the Droseraceae are rather conflicting. The Droseraceae have often been connected with the insectivorous families Sarraceniaceae and Nepenthaceae and classified in Sarraceniales or Nepenthales (Hutchinson 1973; Melchior 1964; Takhtajan 1973; Cronquist 1981). Other families often suggested as close relatives are Saxifragaceae, Crassulaceae and Parnassiaceae.

During the last 120 years there are two opposed opinions as regards the superordinal classification of the family. According to Cronquist (1981) the Droseraceae belong to the Dillenialean alliance. Dahlgren (1980) was initially of the same opinion, but in his revised system (Dahlgren 1983) he agrees with Takhtajan (1973), Heywood (1978) and Thorne (1983) and transferred the family to the Rosalean alliance.

The aim of this study was to enlarge the knowledge of the structure of ovules and seeds of Droseraceae, to draw conclusions concerning the mutual relationships of the genera and to assess the families with which the Droseraceae are related.

MATERIALS AND METHODS

Developing flowers and fruits of *Drosophyllum lusitanicum* L. Link, *Dionaea muscipula* Ellis, *Drosera capensis* L. and *D. intermedia* Hayne were collected in the Hortus Botanicus, University of Amsterdam. Also studied were seeds of *D. capillaris* Poir, *D. natalensis* Diels, *D. rotundifolia* L., *D. regia* Stephens and *D. spathulata* Labill and other species (14 in total).

The plant material was fixed in F.A.A. or Craf mixtures (Sass 1958). Sections were made by the standard microtome technique after embedding in paraffin wax (dehydration in an ethanol/tertiary butyl alcohol series) or in glycol methacrylate (dehydration in an ethanol/n-butyl alcohol series). In the latter case the sections were stained with the periodic acidic Schiff's reaction and counterstained with aqueous toluidine blue (Sidman *et al.* 1961). Phloroglucinol-HCl, Sudan IV, ruthenium red, IKI, and nigrosine solutions were used for the identification of lignins, fats, pectins, starch and proteins, respectively. In order to remove epicuticular wax structures *Drosera* seeds were immersed for 2 h in chloroform.

For scanning electron microscopy (SEM) untreated or critical point-dried specimens were gold- or gold/palladium-sputtercoated for about 2·5 min and studied on a Cambridge stereoscan mark IIa or an ISI DS 130.

RESULTS

Drosophyllum lusitanicum

Ovule development of D. lusitanicum. The ovule primordium is dizonate and consists of the descendants of the original dermal (l_1) and subdermal layer (l_2) of the placenta (Fig. 1a & b). The dermal layer only divides anticlinally and surrounds the subdermal tissue. Shortly before the initiation of the inner integument (ii) the subdermal archespore differentiates (Fig. 1c) and later cuts off 1–2 layers of parietal cells situated as usual above the archespore (Fig. 1d–f). The tetrad is linear and the chalazal megaspore develops into the embryo sac (Fig. 1g). The nucellus becomes massive mainly by periclinal divisions around the embryo sac (es). The inner integument (ii) is initiated dermally as a complete ring-wall two cells broad (Fig. 1c–e) somewhat earlier than, or simultaneously with, the outer integument (oi). The oi is also initiated as a dermal wall two–three cells broad, but the wall is absent at the raphal side or is only represented there by a small dermal cap in the mature ovule.

The ii is at first two–three layered, but it becomes four-layered, mainly by periclinal divisions of its inner layer, when it has overgrown the nucellus. The oi is initially about three-layered (Fig. 1e–g) and remains so until the ovule is mature. Especially in its earlier stages the oi remains much shorter than the ii.

The mature ovule of D. lusitanicum. The ovule is anatropous, bitegmic and crassinucellate. The large nucellus contains a large es. The parietal cells and other cells surrounding the apex of the es have disappeared. The es is probably of the Polygonum type (Fig. 1h).

The ii remains three–four layered and the oi becomes about four-layered by divisions of the middle layer of the originally three-layered integument. The micropyle is formed by the broadened tips of the ii alone (the future operculum), but the oi, which in earlier stages

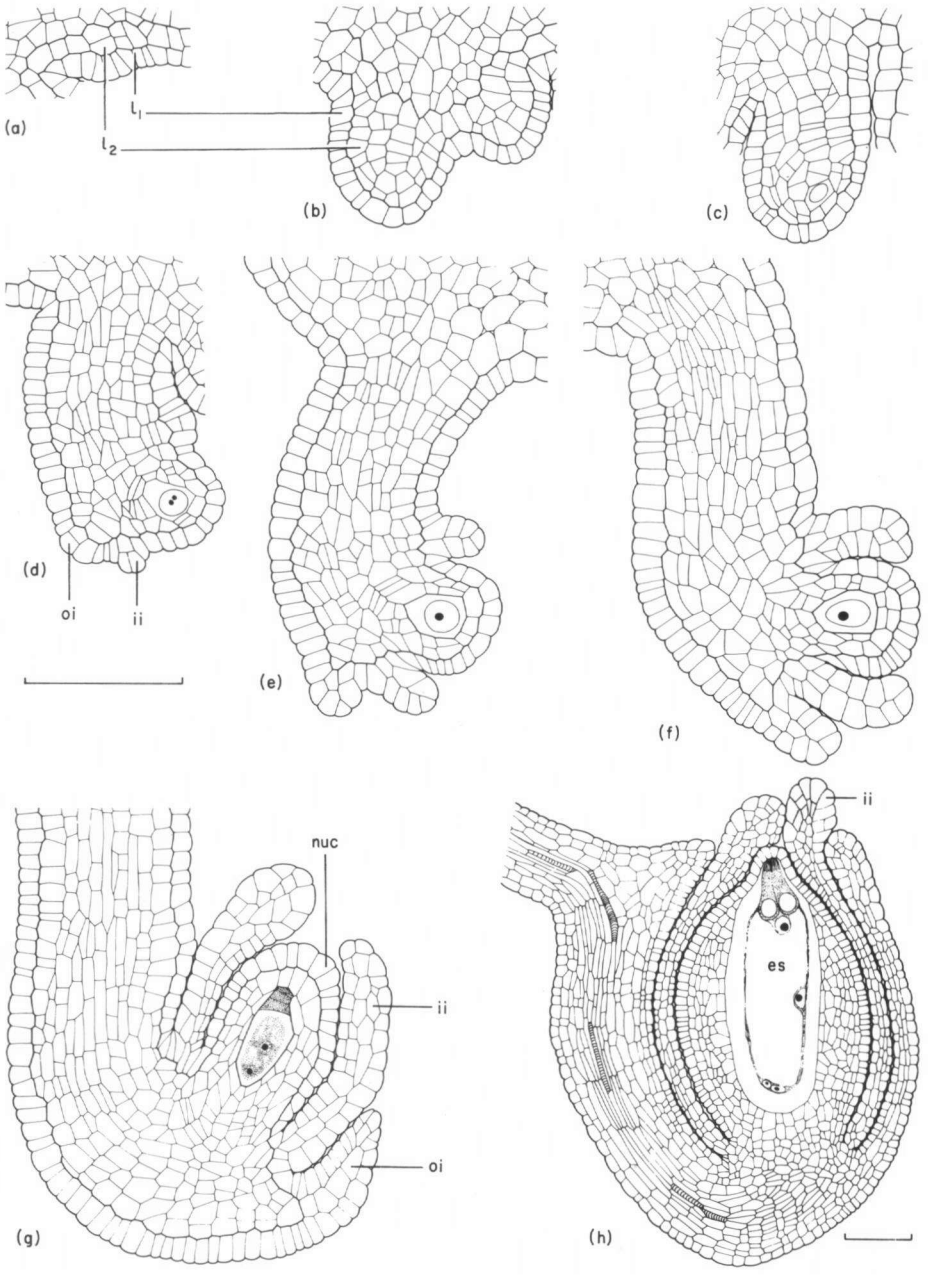

Fig. 1. *Drosophyllum lusitanicum*. Schematical representations of length sections of developing and mature ovules. (a–c) ovule primordia; (d–g) further developmental stages; (h) mature ovule. l_1 and l_2: dermal layer and corpus, respectively. es = embryo sac; nuc = nucellus; ii = inner integument; oi = outer integument. The bars indicate 100 μm; (a–g) at same enlargement.

was much shorter than the ii, has become nearly as long. The amphicribral funicular bundle is distinct and starts to differentiate.

The ovules have very long funicles which are implanted on the apical residuum of the flower. The five styles persist beside a small central opening in the top of the ovary. At pollination this opening is closed by plugs of long multicellular, papillate and pollen-guiding hairs which protrude into the ovarian cavity and are in contact with the chalazal sides of the uppermost ovules. All ovules face to the centre with their raphes.

Seed and seed coat development of D. lusitanicum. After fertilization the ovule increases in size, but its overall shape remains about the same. The endosperm is nuclear and after becoming cellular it fills the embryo sac. Its cells contain numerous starch grains which increase in number and dimension.

The nucellus is compressed, or resorbed, remnants remaining present between endosperm and ii as crushed cells covered by a cuticle (Fig. 2a–e). The ii remains three–four layered (Fig. 2a & b) but later these layers become crushed, except for the inner tanniniferous layer (Fig. 2c). The cells of this endotegmen remain small and isodiametric and become strongly sclerotized with a drop-shaped lumen (Figs 2d & 3d). The tanniniferous cell layers of the tips of the ii (the operculum) are less crushed.

The oi remains four-layered during seed development (Fig. 2a–d). The more densely stained cells of its inner layer enlarge strongly and wall thickenings arise against the inner periclinal walls and parts of the radial walls (Fig. 2c). In the lumen a single large crystal is formed. During further development additional layers of wall thickenings are deposited so that the cell contents are almost completely replaced by wall material, and as a consequence the crystals are pushed against the unthickened outer periclinal walls (Fig. 2d). The endotestal cells are mostly isodiametric but in the narrow apical part of the pyriform seed they are strongly stretched radially. The two middle layers of the oi remain mostly thin-walled, they enlarge and become stretched parallel to the longitudinal axis of the seed (Fig. 2b–d). The outer cells also remain thin-walled but they enlarge perpendicularly to the longitudinal axis of the seed (Fig. 2b–d) and are often grouped in longitudinal rows. At the boundary between the rows the cells may form more or less papillose structures which are grouped in longitudinal ridges on the seed (Figs 2c, 3b & e). At the outside of the seed a distinct, transparent cuticle is gradually formed (Fig. 2b–d).

The mature seed of D. lusitanicum. During the final stages of seed maturation the unthickened outer layers of the oi become crushed and the seed coat shrivels so that the seed surface becomes strongly folded (Figs 2e, 3c & d). The transparent cuticular layer reacts strongly with Sudan IV. The outer cells of the seed coat are filled with a very dark tanniniferous substance (Figs 2e & 3d). The remainder of the seed coat does not change much during the final stages of seed maturation. The sclerotized elements are stained a dark brown. The nucellar cuticle lies against the inside of the endotegmen.

The fleshy endosperm contains many densely packed starch grains reacting strongly with IKI. Their very close contact means that these grains often have flattened facets. The cells of the outer layers of the endosperm are smaller and contain fewer, or hardly any and smaller starch grains, but they contain more protein bodies than the more centrally situated cells. In these more central cells the protein bodies are grouped in the spaces between the starch grains.

The chalazal endosperm cells have an irregular shape; they contain no starch grains and have a large, clear nucleus with several nucleoli or are polynucleate with remains of mitotic spindles. This part of the endosperm has a haustorial character.

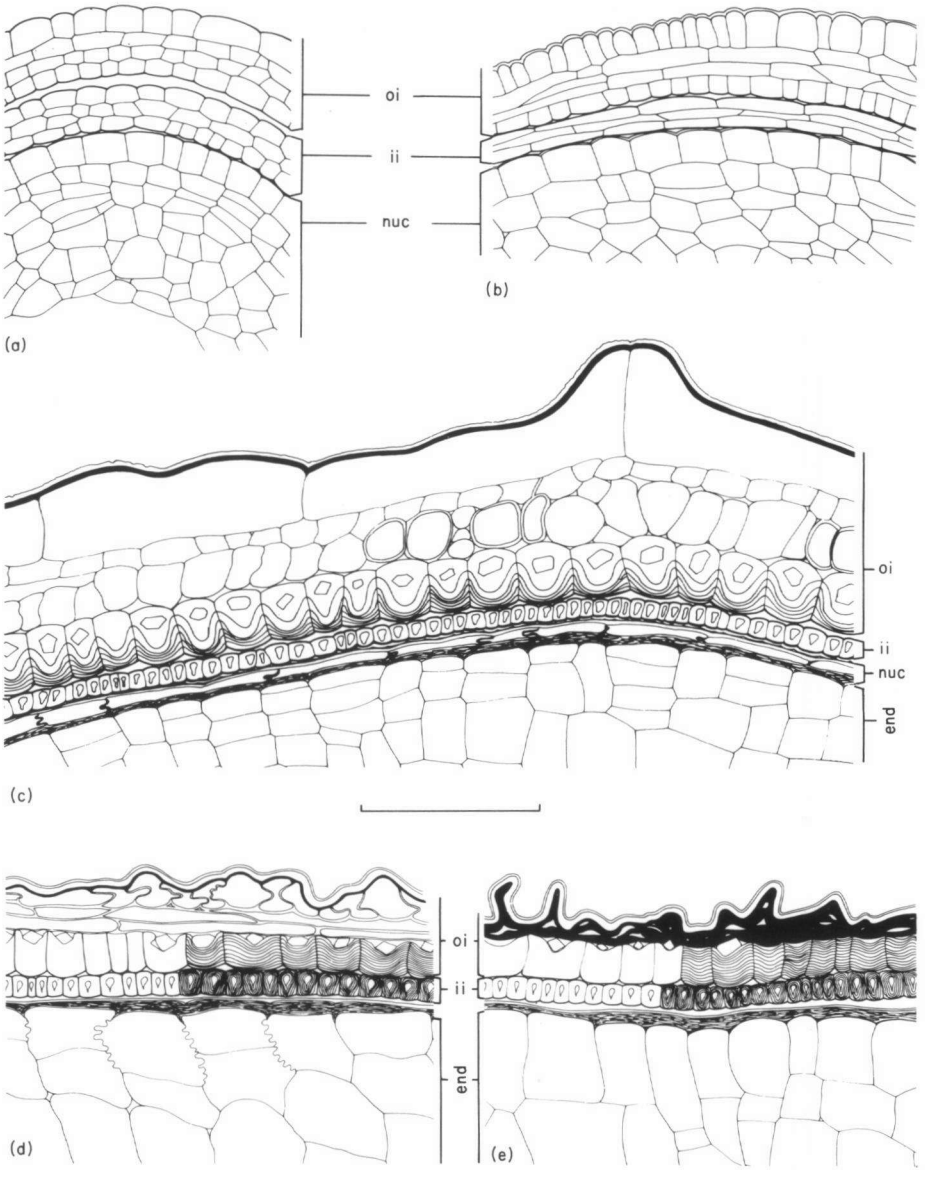

Fig. 2. *Drosphyllum lusitanicum*. Schematical representations of developing seed coats. (a) and (c) cross-sections with, in (c) arising papillose structure; (b), (d) and (e) longitudinal sections; (e) mature seed coat with shrivelled outer layer, endotestal crystal cells and sclerotized endotegmen. Compare with Fig. 3(d). End = endosperm; nuc = nucellus; ii = inner integument; oi = outer integument. The bar indicates 100 μm.

The seed is pyriform and measures about 3 × 2 mm (Figs 3a, e & 8h). The small heart-shaped embryo contains fatty substances and is restricted to the narrow part of the seed below the micropyle. Intercellular spaces have already developed in the cotyledonary tissue of the seed. At germination the top of the ii is lifted as a small operculum and pushed

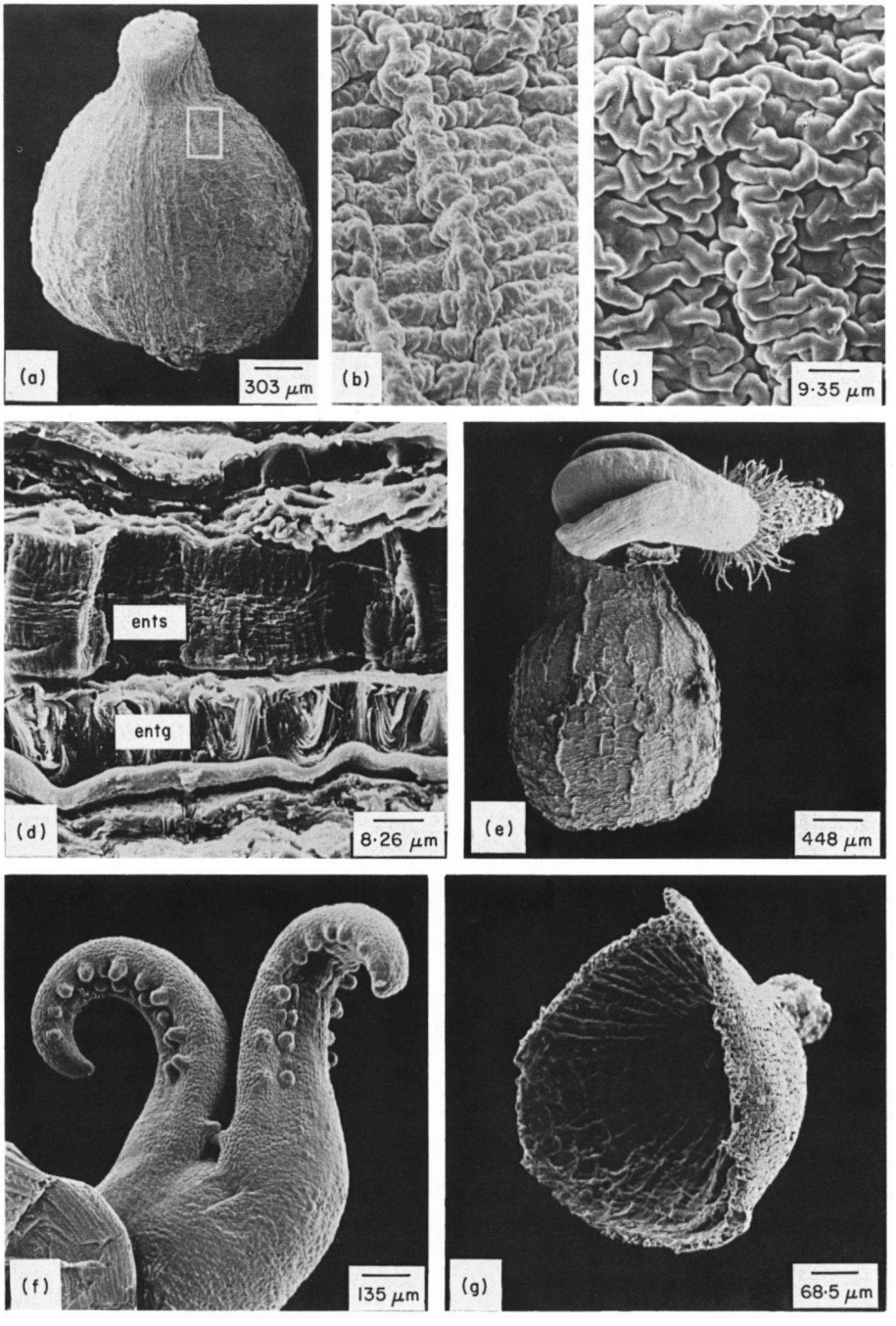

Fig. 3. SEM photomicrographs of *Drosophyllum lusitanicum*, (a) immature seed and (b) enlarged outline figure of testa; (c) surface view of fully mature seed; (d) transverse section of fully mature seed coat with endotesta (ents) and endotegmen (entg); (e) germinating seed with emerging embryo; (f) first leaves of embryo with primordia of glands; and (g) operculum.

out through the orbicular exostome (Fig. 3e & g). The broadened tips of the cotyledons remain enclosed in the seed. The first leaves already show the primordia of the digestive glands (Fig. 3f).

Dionaea muscipula

The ovule and seed of D. muscipula. The placentation of *Dionaea* is basal like that of *Drosophyllum* but the vertical funicles are much shorter. The early stages of ovule development, until megasporogenesis, of *Dionaea* resemble those of *Drosophyllum*, but in later stages the part of the nucellus below the es begins to elongate and the cells of the nucellar epidermis enlarge considerably. When the ovule is mature numerous starch grains are grouped around the nucleus of these cells (Fig. 4f) which constitute a large part of the ovular volume. The central nucellar cells remain small, are somewhat stretched in the length of the ovule and are reminiscent of a conducting tissue. As the result of the stretching of the nucellar base the es becomes situated in the uppermost part of the nucellus (Fig. 8e). The nucellar development can be illustrated by *Drosera capensis*, given in the next section.

The mature ovule is anatropous, bitegmic and crassinucellate. The ii becomes two–three and the oi three–four layered (Fig. 4f). The outer layer of the oi already starts to differentiate into the mechanical layer of the seed coat.

The fully mature, black and shiny seeds (Fig. 4a) are embedded in the placenta. The exotestal cells with black, thickened walls are stretched radially. The anticlinal walls are strongly thickened and more or less reticulate by large pits. The inner periclinal and the lower parts of the anticlinal walls remain thin (Fig. 4b–d). The remaining inner layers of the oi, together with the outer layers of the ii are crushed, except for the inner layer of the ii which consists of tangentially flattened, tannin containing cells. Between this layer and the endosperm there is a nucellar cuticle. The endosperm contains many densely packed starch grains.

The seed of *Dionaea* has the same general structure as that of *Drosophyllum*. The small embryo is situated below the micropyle and the top of the ii forms a sclerotized operculum which is lifted at germination (Figs 4e & 8f). At germination the inflexible seed coat may fall into several pieces. The two green cotyledons are gradually pushed out, but their tips initially remain within the seed. The third normal leaf already develops into a small, complete two-lobed trap. An adventitious root starts to develop early from a higher stem part.

Drosera capensis

Ovule development of D. capensis. The ovule primordium of *D. capensis* is dizonate (Fig. 5a–c). It is very small at first, about four cell layers thick, in longitudinal section, and consists of a dermal layer which surrounds a central core of four cells in cross-section (Fig. 5b).

The archespore differentiates at the moment of the initiation of the ii and soon cuts off a parietal cell. The tetrad is linear and the chalazal megaspore develops into the es. Shortly before the ovule is mature the lower part of the nucellus becomes stretched and the dermal cells enlarge considerably (Fig. 5i–l). The central nucellar cells remain small and apparently form a conductive strand from the chalaza to the es. These conductive cells are the descendants of the central cells of the ovule primordium which can be seen in cross-section (Fig. 5b & l). In both cases there are four central cells.

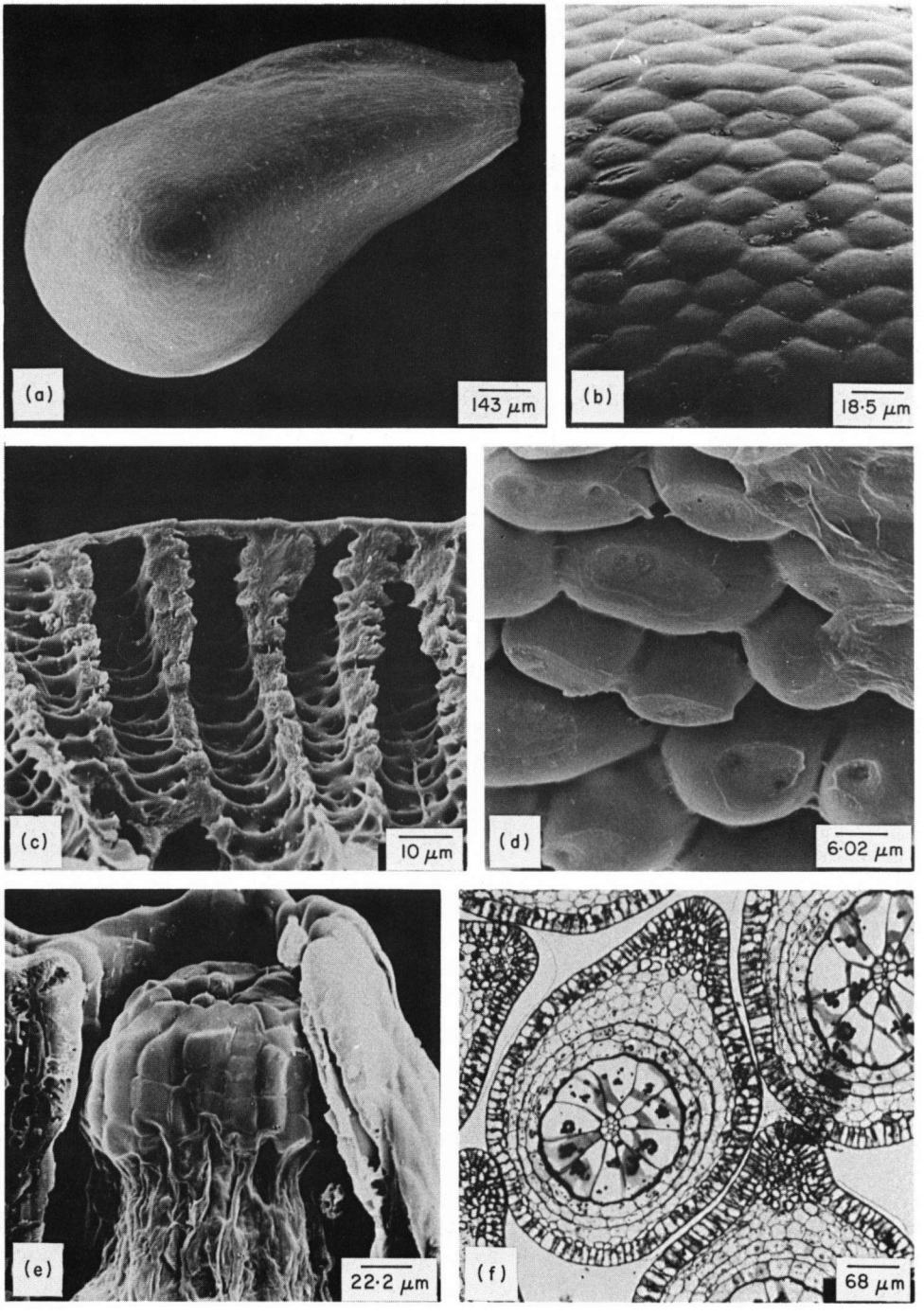

Fig. 4. *Dionaea muscipula.* SEM (a–e) and light-microscopical (f) photographs. (a) Seed and (b) detail of seed surface; (c) transverse section and (d) inner boundary of exotesta; (e) view of operculum after removal of part of testa. (f) Transverse section of mature ovule, with swollen cells of the nucellar epidermis and starting differentiation of exotesta.

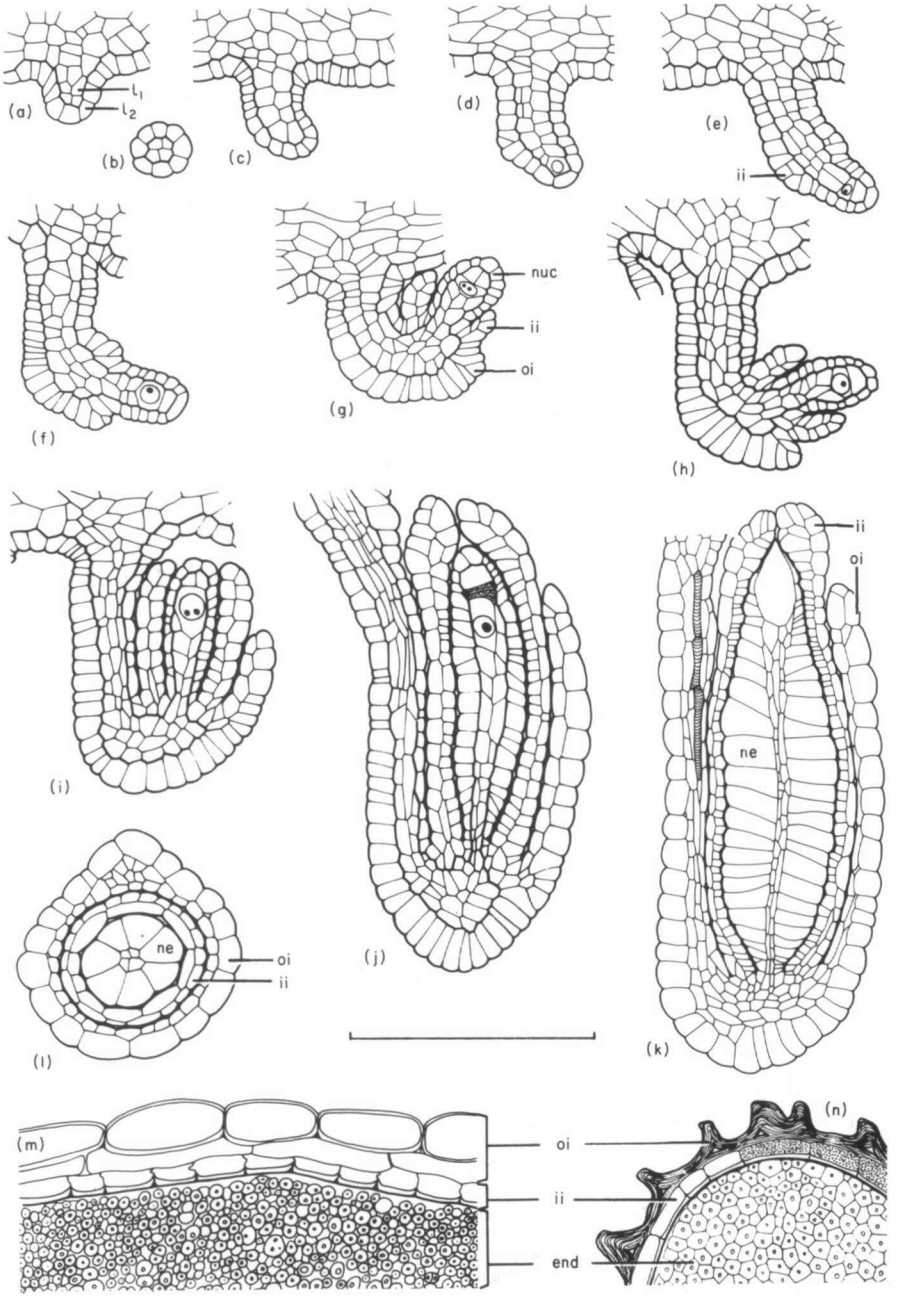

Fig. 5. *Drosera capensis*. Schematical representations of ovule and seed coat development. (a–j) Developing ovules: longitudinal sections including a cross-section; (b) mature ovule, (k) longitudinal and (l) transverse section with large cells of the nucellar epidermis and small inner cells, es in nucellar top; (m) length section of developing seed coat; (n) mature seed coat: transverse section with collapsed exotesta and tanniniferous endotegmen. es = embryo sac; end = endosperm; nuc = nucellus; ne = cells of the nucellar epidermis; ii = inner integument; oi = outer integument; l_1 and l_2: subdermal and dermal layer. The bar indicates 100 μm.

The ii and oi are initiated as ring-walls, the ii somewhat earlier than the oi, of which the wall is suppressed at the raphal side. Both integuments are two-layered and the oi is shorter than the ii (Fig. 5f–j).

The fully developed ovule of D. capensis. The ovule is anatropous, bitegmic, crassinucellate and longitudinally stretched (Fig. 5k). The es is situated within the nucellus top. The cells of the nucellar epidermis except the dermal cells around the es, are very large, and those at the nucellus top have disappeared. These large dermal cells constitute the greater part of the ovular volume. Starch grains are grouped around their nuclei.

The integuments are two-layered and the tip of the ii (the future operculum) has broadened and protrudes above the oi so that the micropyle is formed by the endostome. The cells of the outer layer of the oi are large and contain tannins, as do the cells of the inner layer of the ii. The distinct raphal bundle starts to differentiate.

Seed development and the mature seed of D. capensis. During seed development the elongated shape of the seed is accentuated by the outgrowth of the exostome and chalaza, making the mature seed spindle-shaped (Fig. 6a). The enlarged cells of the nucellar epidermis have been crushed and resorbed and their space has become occupied by embryo and endosperm. The endosperm formation is nuclear and becomes cellular later, and the cells are ultimately filled with densely packed starch grains (Fig. 5m & n). By their close contact the starch grains assume a more polygonal form.

The cells of the inner layer of the ii contain tannins, stretch somewhat perpendicularly to the longitudinal axis of the seed, and their inner and partly their radial walls become slightly thickened (Fig. 5k–n). Against the inside of these thickened walls the nucellar cuticle is still present. The cells of the outer layer of the ii disappear first, followed by those of the inner layer of the oi. The tanniniferous cells of the outer cell layer of the seed enlarge strongly and the outer walls are pressed against the inner ones. The radial walls are responsible for the reticulate pattern of the seed surface (Figs 5m, n & 6a & b). The outer wall is covered by a cuticle containing waxy substances, and small wax particles are present (Fig. 6b).

The seed is provided with surface enlargements at both ends (Figs 6a & 8b). At the micropyle an air sac is formed by the strong outgrowth of the oi after fertilization, so that in the mature seed the oi is much longer than the ii. At the chalazal end an outgrowth originates which, after the formation of intercellulars and/or disintegration of cells, becomes shrivelled (Fig. 8b).

When the seed germinates the root grows through the tube of the oi often with the operculum (Fig. 6e) at its tip.

Seed morphology of some Drosera *species.* The seeds of other *Drosera* species show marked differences in shape, size and micromorphology. In the 14 species studied the seed size varies from about 450 μm in *D. intermedia* (Figs 6d & 8c). *D. spathulata* (Fig. 7e). *D. binata, D. indica* and *D. montana,* to about 1700 μm in *D. rotundifolia* (Figs 7a & 8d). However, these differences in size are caused mainly by the extent of the micropylar and chalazal outgrowths.

Whereas in *D. rotundifolia* (Figs 7a & 8d) and *D. natalensis* (Fig. 7c) both micropyle and chalaza are extended distinctly, in *D. intermedia* (Fig. 6d), *D. anglica, D. capillaris* and *D. indica* only the micropyle is extended and in *D. regia* (Fig. 7f) mainly the chalaza has

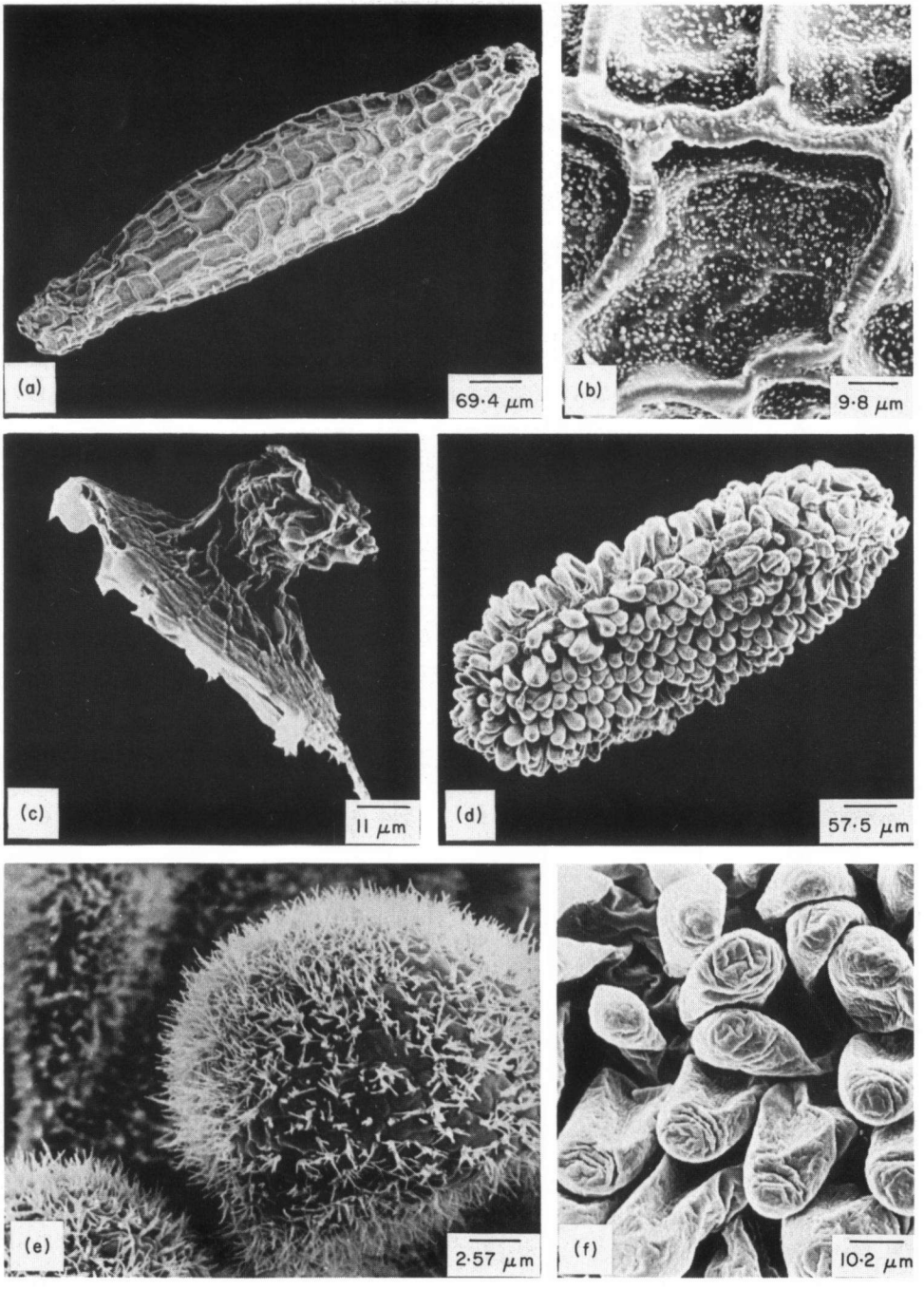

Fig. 6. SEM photomicrographs of *Drosera* seeds. *D. capensis*, (a) seed and (b) detail of testa; (c) operculum; *D. intermedia*, (d) seed and (e) enlarged papillae with wax rods; (f) wax particles removed with chloroform.

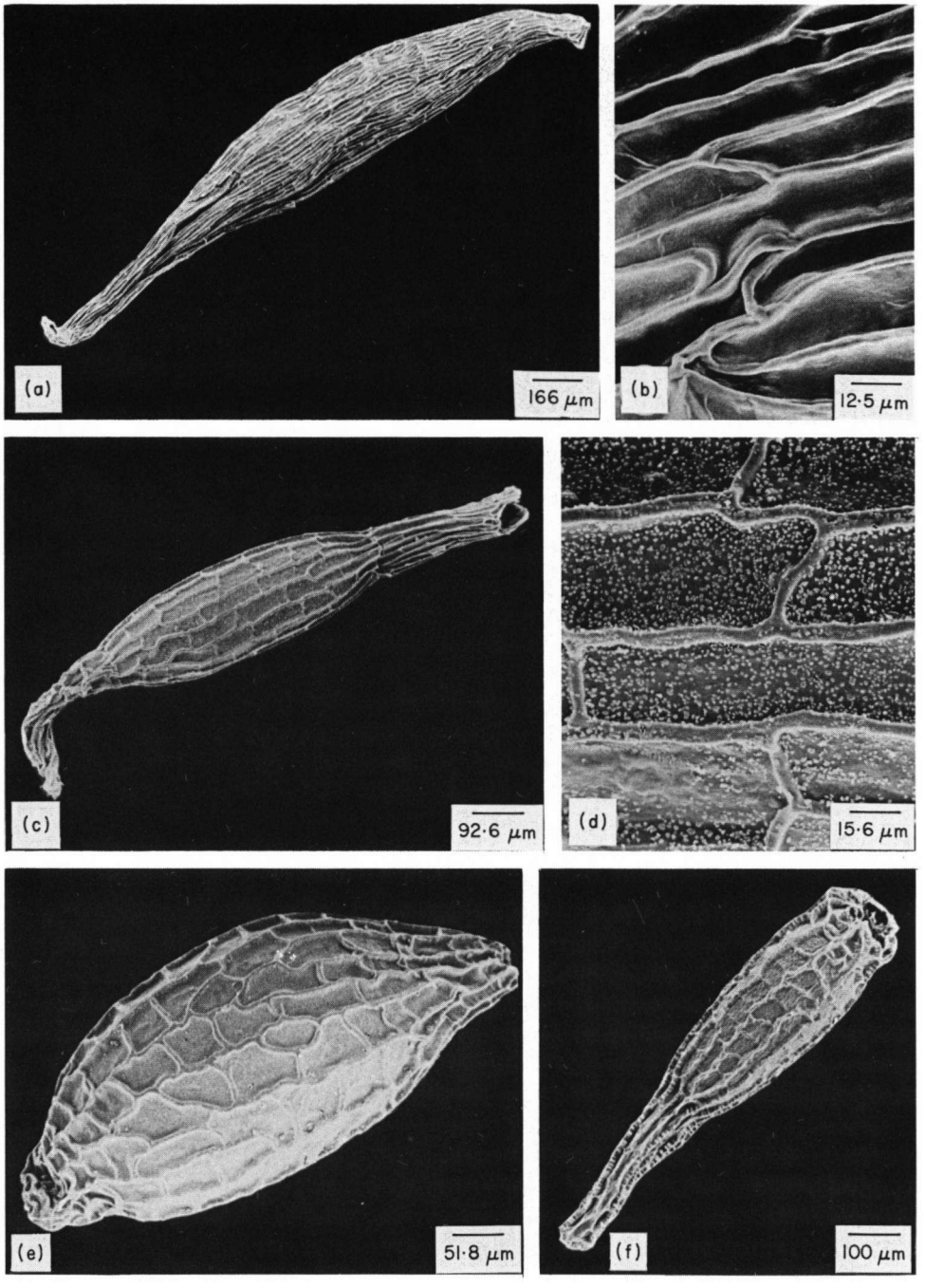

Fig. 7. SEM photomicrographs of *Drosera* seeds. *D. rotundifolia*, (a) seed and (b) detail of testa; *D. natalensis*, (c) seed and (d) detail of testa with wax particles; (e) *D. spathulata* and (f) *D. regia* seeds.

become elongated. In *D. spathulata* (Fig. 7e), *D. montana, D. curviscarpa, D. ramentacea* and *D. villosa* the micropyle and chalaza are only slightly extended.

In all species studied the seed body consisting of embryo and endosperm has about the same dimensions, the length–width ratio varies from 1·5 to 3·0 and the length from 300 to 500 μm. The seed coat anatomy, as far as could be seen, is the same in all *Drosera* species.

The micromorphology of the seed surface shows variations in the shape and pattern of the exotestal cells and epicuticular waxes. The seed surface of *D. natalensis* and *D. spathulata*, like that of *D. capensis*, is covered with wax particles which dissolve in chloroform (Fig. 7c–e). The seed coat of *D. rotundifolia* has a smoother surface without such particles (Fig. 7b). The seed of *D. intermedia* differs from the species mentioned above and its tanniniferous outer cells are not collapsed but have grown out into papillae. The latter are covered with wax rods (Fig. 6e) which dissolve completely when the seed remains in chloroform for about 2 h (Fig. 6f). The seed of *D. capillaris* is similar to that of *D. intermedia* in having papillae on its outside covered with wax particles.

A comparison of the seeds of Drosophyllum lusitanicum, Dionaea muscipula, Drosera capensis, D. intermedia *and* D. rotundifolia

The mature seeds of the genera *Drosophyllum, Dionaea* and *Drosera* correspond much in their general structure (Fig. 8b–d, f & h) but differ in their dimensions and seed coat structure. The seeds of *Drosophyllum, Dionaea* and *Drosera capensis* have a length of about 3, 1 and 0·6 mm respectively. Similar features include: the small embryo situated under the micropyle, the starchy endosperm, and the operculum formed by the tips of the ii and lifted during germination. The tops of the cotyledons have a haustorial function and remain within the seed during germination.

The ontogenetic potential of the ovule of *Drosophyllum* is the largest, the seed becoming four times as long as the ovule (Fig. 8g & h). The ovule of *Dionaea* is almost as large as that of *Drosophyllum*, but the seed is smaller, only twice the length of the ovule (Fig. 8e & f). The ovule of *D. capensis* (Fig. 8a) is the smallest, only half that of *Drosophyllum* and *Dionaea*. *Drosera* has the smallest seeds of all Droseraceae (Fig. 8b). The seed of *D. capensis* is about twice the length of the ovule.

DISCUSSION

The ovules and especially the operculate seeds with fleshy and starchy endosperm of *Drosophyllum, Dionaea* (Smith 1929), *Aldrovanda* (Teryokhin 1986) and *Drosera* are very similar. The seed coat structure of Droseraceae with a thick- or thin-walled endotegmic pigment layer and a crushed outer tegmen is also essentially the same in all genera. The anatomical characters of the seed support the placement of the four genera in one family Droseraceae.

For the first time a complete description of ovule and seed development of *Drosophyllum* is presented. The ovule and seed of *Drosophyllum* are the largest and the seed coat the most complex in Droseraceae. *Drosophyllum* has a very distinct crystalliferous endotesta. According to Corner (1976) the seed coat of *Drosophyllum* is exotegmic, but this suggestion is based on an incorrect interpretation of Netolitzky's (1926) incomplete description. In this study it is shown that the tegmen is only represented in the mature seed coat by a layer of small isodiametric, sclerotized endotegmic cells.

The ovule of *Dionaea* is nearly as large as that of *Drosophyllum* but it differs much from the latter in the strongly enlarged cells of the nucellar epidermis and in the stretching of the

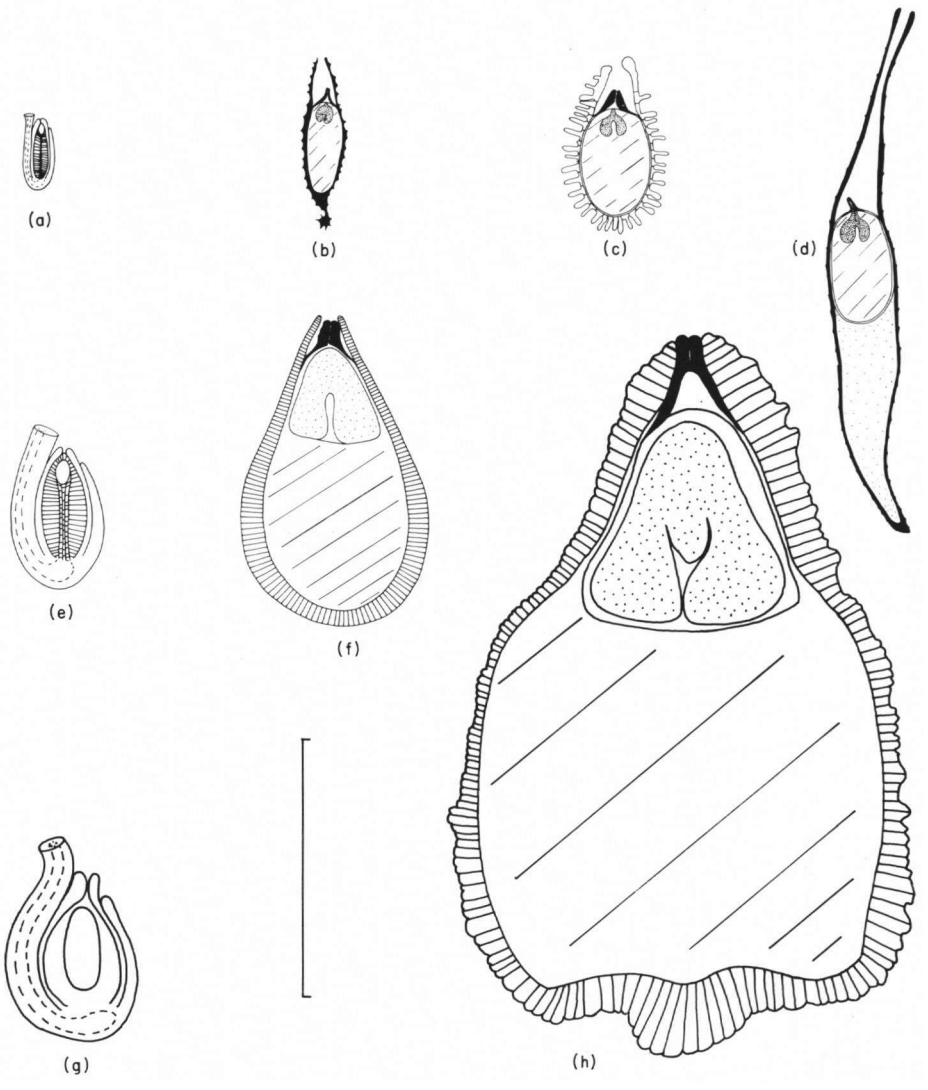

Fig. 8. Longitudinal sections of mature ovules and seeds of *Droseraceae*. *Drosera capensis*, (a) ovule and (b) seed; (c) *D. intermedia* and (d) *D. rotundifolia* seeds; *Dionaea*: (e) ovule and (f) seed; *Drosophyllum*: (g) ovule and (h) seed, operculum drawn in black. The bar indicates 1 mm for all figures.

lower part of the nucellus as a result of which the es becomes localized within the nucellar top. The seed coat is exotestal and the other seed coat layers are crushed.

The ovule of *Aldrovanda* is similar to that of *Dionaea* (Teryokhin 1986). The exotesta has comparable, reticulate thickened walls. In *Aldrovanda* a non-crystalliferous endotesta is also present. *Aldrovanda* is probably more closely related to *Dionaea* because of the similarities in the seed coats and the two-lobed traps.

The ovule of *Drosera* is of the same type as that of *Dionaea*, with very large cells of the nucellar epidermis, but it is much smaller. Also the seeds, which are often dust seeds, are the smallest of all Droseraceous genera.

If large ovules and seeds and a complex seed coat are pleisomorphic, and small ovules, ovules with enlarged nucellar epidermal cells, small seeds and a less complex or simplified seed coat may be considered apomorphic characters, the following conclusions can be drawn.

(i) *Drosophyllum* is the most original genus, with a normal ovule and a large seed with a complex seed coat. This conclusion is supported by the slightly woody stem with secondary growth, the normal root development (Diels 1906), the dispersal of the pollen as separate grains (not united in permanent tetrads as in the other three genera) and the immobile tentacles. These characters, which may partly be related with its dry environment, separate *Drosophyllum* from the rest of the family. Takahashi & Sohma (1982) even conclude, erroneously according to us, on the grounds of the separate dispersal of the pollen grains and differences in pollen grain structure, that *Drosophyllum* is not related to other members of the Droseraceae.

(ii) *Dionaea* and probably also the rootless water-plant *Aldrovanda* are more derived than *Drosophyllum*, because of the ovules with enlarged cells of the nucellar epidermis, the smaller seed, less complex seed coat, and the complicated trap.

(iii) *Drosera* is the most advanced of all genera because of its very small derived ovules, the small seed dimensions, the simple seed coat and the lack of a main root (Heinricher 1902; 1903; Diels 1906).

(iv) *Drosophyllum* and *Dionaea* have a basal, and *Aldrovanda* and *Drosera* a parietal placentation. If *Drosophyllum* is indeed the most original and *Drosera* the most derived genus, basal placentation may be original in the family and parietal placentation derived.

(v) Parietal placentation has the advantage of a large placental surface allowing for the production of many small seeds such as in *Drosera*.

(vi) The enlarged cells of the nucellar epidermis are an advantage, because this represents an efficient way to obtain a more voluminous nucellus which, after crushing, offers the necessary space for endosperm and embryo.

(vii) *Drosera* seeds are very small dust-seeds provided with air sacs and are typically suited to wind dispersal although secondary dispersal by water must not be ruled out (Holzner 1902). According to Skogen (1979) water fowl are the main distribution agents in long-distance dispersal in *D. intermedia*. The turions of *Aldrovanda* may also be dispersed exozoochorously by water-birds (Berta 1961). Dispersal by birds may well explain the large area of distribution of *Drosera* species (Schnell 1970) and *Aldrovanda*.

The family Droseraceae is a relatively old, although derived family. Its remains are found from the Eocene onwards (Muller 1981) and possibly from the late Cretaceous (Knobloch & Mai 1984). Derived characters are the carnivorous habit, the dizonate ovule primordium and the specialized seed structure and mode of germination. The tips of the cotyledons are broad in all genera. This may be associated with the haustorial function of these tips. Broad cotyledons easily remain behind in the seed because their passage through the opening by which the root emerges is difficult.

Unfortunately the characters of ovule and seed coat do not provide conclusive evidence for the taxonomic relationships of the family and cannot solve the existing differences in opinion.

As regards families of dilleniid affinities the Begoniaceae resemble the Droseraceae with their ovules with large nucellar epidermis cells and their operculate seeds (Boesewinkel & de Lange 1983). However, the Begoniaceae seeds are exotestal, have a large embryo with only one layer of endosperm and the operculum is mainly formed by the tips of the oi.

Within the Rosalean affinity the Crassulaceae also have enlarged nucellar epidermis cells (Rombach 1911).

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