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DEVELOPMENT OF OVULE AND SEED IN MARANTACEAE

C.J. GROOTJEN

Hugo de Vries-Laboratorium, Plantage Middenlaan 2a, 1018 DD Amsterdam

SUMMARY

The development of ovule, seed and seed coat in a few representatives of the Marantaceae was studied. A subdermally initiated outer integument was found in a monocotyledon for the first time. The seed, which belongs to the most complex among the monocotyledons, is campylotropous and, furthermore, characterised by a so-called perisperm channel, an operculum, micropylar collar and aril, the latter having a function in fruit dehiscence. The mature seed coat consists mainly of a silicified endotesta covered by tanniniferous cells, derived from the inner and the middle layers of the outer integument, respectively.

1. INTRODUCTION

The tropical family of the Marantaceae contains about 400 species and forms a well-defined and very natural group which is considered to be strongly advanced among the Zingiberales.

The structure of the marantaceous ovule has been relatively well described (see GRIS 1859, 1860, HUMPHREY 1896, SCHACHNER 1924, NETOLITZKY 1926, VENKATASWARALU 1937, DAVIS 1966): the ovule is anacampylotropous, crassinucellate, with a two-layered inner and a multi-layered outer integument; the micropyle is usually formed by the inner integument alone. Characteristic features are cell elongation and periclinal divisions in the apical epidermis of the nucellus.

There is, however, not so much information concerning the ontogeny and the anatomy of the seed which is one of the most highly differentiated among the monocotyledons (see GRIS 1860, EICHLER 1884, HUMPHREY 1896, NETOLITZKY 1926). Out of the anacampylotropous ovule a completely campylotropous seed develops by unequal growth of the nucellar tissue. A proliferation of the chalaza and the nucellus results in the penetration of the chalaza into the nucellar body. The structural features of this ingrowth have been summarily described by SCHACHNER (1924). During seed maturation the chalazal ingrowth degenerates and the nucellus forms the perisperm, so that a hollow "perisperm channel" orginates. The shape of this channel varies and has taxonomic significance: three types have been distinguished by ANDERSSON (1981), *viz.*, a straight unbranched one; a straight, distally ramifying one whose branches partly embrace the curvature of the embryo; and a basally branched one whose ramifications lie parallel to the curved embryo. Additional characteristics of the marantaceous seed are the operculum, micropylar collar, and arillus, all three struc-

tures typical of the Zingiberales (MAURITZON 1936). The aril plays a role during fruit dehiscence (MÜLLER 1883, SCHUMANN 1902, ANDERSSON 1981) and also in seed dispersal (by myrmecochory, see HORVITZ & BEATTIE 1980). The principal seed coat layer is the innermost layer of the outer integument (an endotesta sensu CORNER 1976); the inner integument is crushed and obliterates. As regards the fate of the remaining layers of the outer integument opinions are divided (NEES VON ESENBECK 1831, HUMPHREY 1896, RODE 1913, SCHACHNER 1924, NETOLITZKY 1926, MAURITZON 1936).

The present study aims at a detailed description of the ontogeny and the anatomy of the ovules and seeds of some Marantaceae.

2. MATERIALS AND METHODS

The material of the species *Calathea picturata* (Lind.) K. Koch et Lind., *Thalia dealbata* Fraser, *Pleiostachya pruinosa* (Regel) K. Schum. and *Maranta leuconeura* Morren was collected in the Botanical Garden, University of Amsterdam and fixed in Allen's Modified Bouin Fluid. After fixation the material was transferred to and kept in 70% ethanol until processed further. Of the two first-mentioned species a whole series of developmental stages was studied, of the other two only the pre-fertilisation stages. Additional spirit material of post-fertilisation stages of *Ischnosiphon, Maranta* and *Stromanthe* species was kindly provided by Dr. Lennart Andersson (Göteborg).

For standard transmission microscopy the fixed material was dehydrated in a NBA series, embedded in glycolmethacrylate, microtomed at 5 μm and stained with PAS and hematoxylin.

The SEM studies were carried out by means of a Cambridge Stereoscan Mark 2a. The younger developmental stages were, from the 70% ethanol, first dehydrated in an alcohol series to absolute ethanol and subsequently critically point-dried and sputtered; older stages and mature seeds were directly SEM-studied after or without sputtering.

3. RESULTS

3.1. Ovule ontogeny

The marantaceous ovary is trilocular with in principle one basally inserted ovule per locule, as in *Calathea picturata.* In *Pleiostachya pruinosa, Thalia dealbata* and *Maranta leuconeura* only one of the locules is fertile. The position of this fertile locule varies: in *Pleiostachya* it is the posterio-median one, and in the two other species the anterio-median locule. Unless otherwise indicated the following details refer only to *P. pruinosa.*

The placental area is dizonate, *i.e.,* it consists of a periclinally dividing corpus surrounded by an initially only anticlinally dividing tunica layer *(fig. 1).* After ovule initiation a second, subdermal tunica layer originates from the corpus;

the ovule primordium is, accordingly, secondarily trizonate (see *fig. 2*).

The subdermal archespore cell is already discernible at this stage and soon divides into the megaspore mother cell and the primary parietal cell *(fig. 3)*, the latter dividing repeatedly *(figs. 4–6)* to form a one-layered parietal tissue which already becomes obliterated before fertilisation.

The inner integument is initiated as a complete, two-layered ring wall in the dermal layer of the young ovule *(figs. 3, 4)*, in older stages it becomes pluri-layered distally *(figs. 5–7)*.

The first cell divisions leading to the formation of the outer integument likewise occur in the dermal layer, but soon already also divisions take place in the subdermal layer *(fig. 3)* and the subsequent growth of the integument takes place in its subdermal part *(figs. 4–7)*. Although the outer integument develops to a much lesser extent at the raphal side of the ovule, also in that zone numerous cell divisions take place *(fig. 3)* especially in the dermal layer *(figs. 4, 5)*. This ultimately results in a pluri-layered mass of tissue of dermal derivation at that flank of the ovule *(figs. 6, 7)* extending to the zone of attachment of the inner integument. The outer integument is initially about six cell layers thick, but later on periclinal divisions around the micropyle render that ovular part multi-layered *(fig. 7)*. The outer integument remains shorter than the inner one, so that the micropyle is formed by the inner integument alone.

The anatropous curvature of the ovule already becomes discernible during the integument initiation *(fig. 3)*. Initially the bending continues *(figs. 4, 5)* but in later stages the nucellus grows asymmetrically by developing more strongly at the anti-raphal side *(fig. 6)*. Owing to this differential growth process the mature ovule becomes anacampylotropous *(fig. 7)*. The nucellar tissue surrounding the embryo sac contains starch grains. The nucellar epidermis has in the mean time formed a "nucellar pad": the apical cells have become stretched in the radial direction and in the adjacent cells also periclinal division occur; these cells also have thickened inner walls which are not found in the apical ones *(fig. 24, Calathea picturata)*. The funicle has a papillose epidermis and presumably functions as an obturator.

The ovular ontogeny of the other three species proceeds along very similar lines. The outer integument is also subdermally initiated. However, the dermal mass of tissue in the raphe is far less opulently developed than it is in *Pleiostachya* and does not reach further than the apex of the nucellus. In mature ovules *(figs. 8–10)*, apart from minor details such as the presence of starch in the nucellus and embryo sac *(fig. 8)*, especially the variation in developmental stages is striking. This variation is not only expressed in the overall size but also in the rate of campylotropy and in the differentiation of the exostome area, which processes will be discussed below.

3.2. Campylotropy

Before and after the time of fertilisation a special development takes place ultimately resulting in a truly campylotropous seed. The primary cause is a strongly asymmetrical growth of the nucellus: the anti-raphal side grows much faster

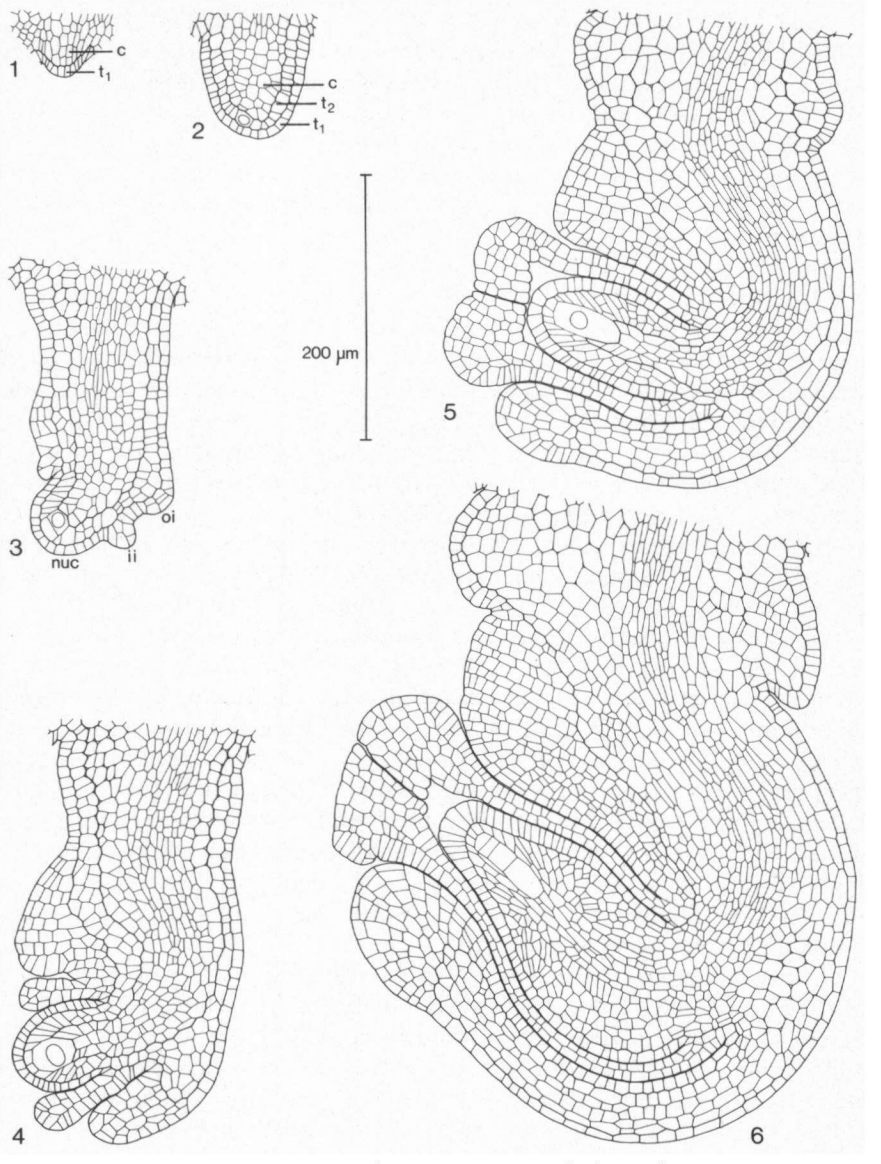

PLATE I. Figs. 1–6: Longitudinal sections of developing ovules of *Pleiostachya pruinosa*. The young ovule is secondarily trizonate. The inner (ii) and outer integument (oi) are of dermal and subdermal derivation, respectively. The curvature of the ovule is initially anatropous; in fig. 6 the campylotropous bending, caused by unequal growth of the nucellus, commences.
c = corpus, nuc = nucellus, t_1 = dermal tunica layer, t_2 = subdermal tunica layer.

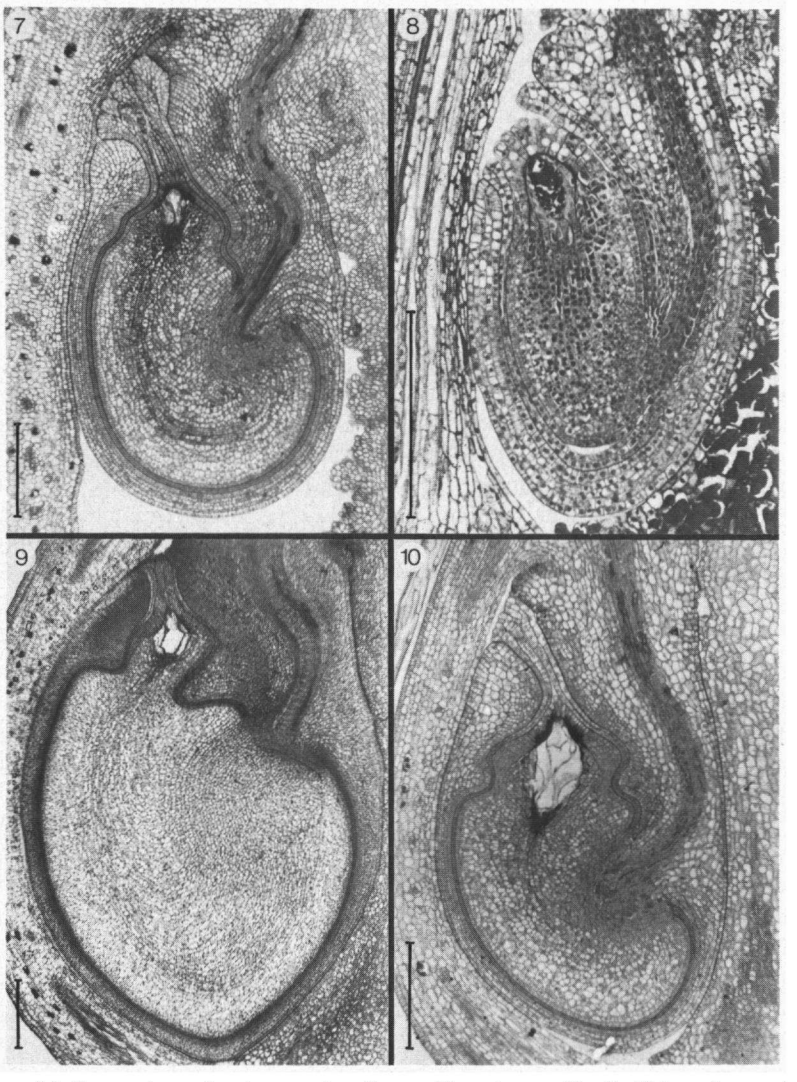

PLATE II. Median sections of mature ovules of some Marantaceae. Fig. 7: *Pleiostachya pruinosa;* fig. 8: *Maranta leuconeura;* fig. 9: *Thalia dealbata;* fig. 10: *Calathea picturata.* Note the variation in developmental stages. Magnification bars represent 200 μm.

than the opposite one. This can be illustrated by the lengths ratio of the antiraphal and raphal flanks of the nucellus, which is still 1 in the young ovule shown in *fig. 5* to rise to 1.5 and 4, respectively, at the stages shown in *figs. 6* and *7*. In *Calathea picturata* this ratio increases to 10 in the seed stage *(fig. 11)*. Since the nucellar growth initially takes place especially in the basal antiraphal area, the chalaza thus becomes partly surrounded by nucellar tissue. The central axis of the nucellus shifts and progressively bends, which bending is increased by the growth in length of the tissue included in the curvature. In *Calathea (fig. 11)* and in other genera with a straight chalazal intrusion such as *Maranta, Stromanthe* and *Ischnosiphon*, this tissue is of chalazal derivation, but in *Thalia (fig. 9)*, in which the chalazal intrusion bends in unison with the axis of the nucellus, it is of nucellar origin.

In the post-fertilisation stage, apart from other cell types, within the nucellus especially the cells later resorbed by the embryo sac are clearly discernible because they start showing autolysis already at an early stage. The embryo sac does not develop along the original longitudinal axis of the nucellus. A peculiarity of the embryo sac development in *Calathea picturata* is that the antipodal cells persist till long after fertilisation. The endosperm is nuclear and is ultimately completely resorbed by the developing embryo. The main reserve nutrient for the embryo is the starch in the perisperm.

3.3. Development of the perisperm channel

a. *Calathea picturata*

During the ovular ontogeny a procambium strand consisting of extended, plasma-rich cells develops in the funicle and raphe *(fig. 10)*. Its cross-sectional shape varies from elliptic in the funicle to a C-shape with hollow side facing the micropyle in the micropylar region to become, finally, circular towards the chalaza. By the time of fertilisation, starting from the funicular end, phloem and xylem elements begin to differentiate. The xylem consists of vessels and tracheids with annular wall thickenings and lies at the inner side surrounded by an arch of phloem elements.

In connection with the campylotropous curvature the chalaza becomes partly enclosed by the nucellus after fertilisation (see *fig. 11*), as is evident from the position of the zone of insertion of the integuments which comes to lie within the nucellus. Concomitantly a strong growth of the enclosed part of the chalaza commences which results in an intrusion of chalazal tissue, in which chalazal ingrowth the procambium strand continues to differentiate (*figs. 11* and *12*). The procambial strand is surrounded by parenchyma. The border line between the chalazal tissue and the nucellus is formed by a sheath consisting of several layers of small cells rich in cytoplasm.

At an older stage (see *fig. 13*) the chalazal intrusion broadens at the distal end, the number of vascular elements of the central vascular bundle complex increasing at the same time and becoming arranged in small groups. The parenchyma is strongly vacuolised and contains conspicuous intercellular spaces especially at the side facing away from the embryo sac. Within this parenchyma

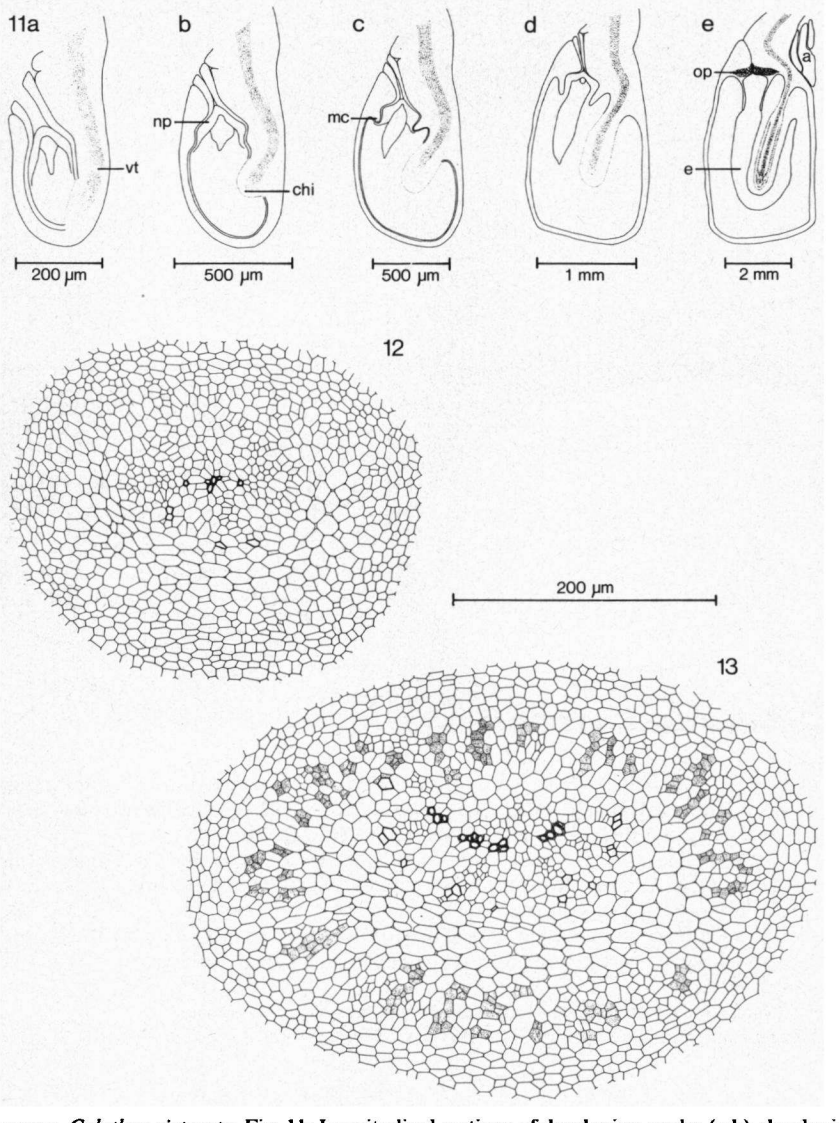

PLATE III. *Calathea picturata*. Fig. 11: Longitudinal sections of developing ovules (a,b), developing seeds (c,d) and a nearly mature seed (e), showing the intrusion of chalazal tissue (chi) into the nucellus and the campylotropous curvature. The rate of campylotropy, expressed as the lengths ratio of the anti-raphal and raphal sides of the nucellus, is 1.7, 3.2, 5.5, 7, and 10, respectively.
a = aril, e = embryo, mc = micropylar collar, np = nucellar pad, op = sclerotic part of the operculum, vt = provascular or vascular tissue. Figs. 12–13: Cross section of the chalazal intrusion of developing seeds corresponding with figs. 11c and 11d. The embryo sac is situated above. In the centre of the ingrowth groups of xylem and phloem elements differentiate. Later on, a peripherally lying ring of provascular strands (dotted) originates (fig. 13).

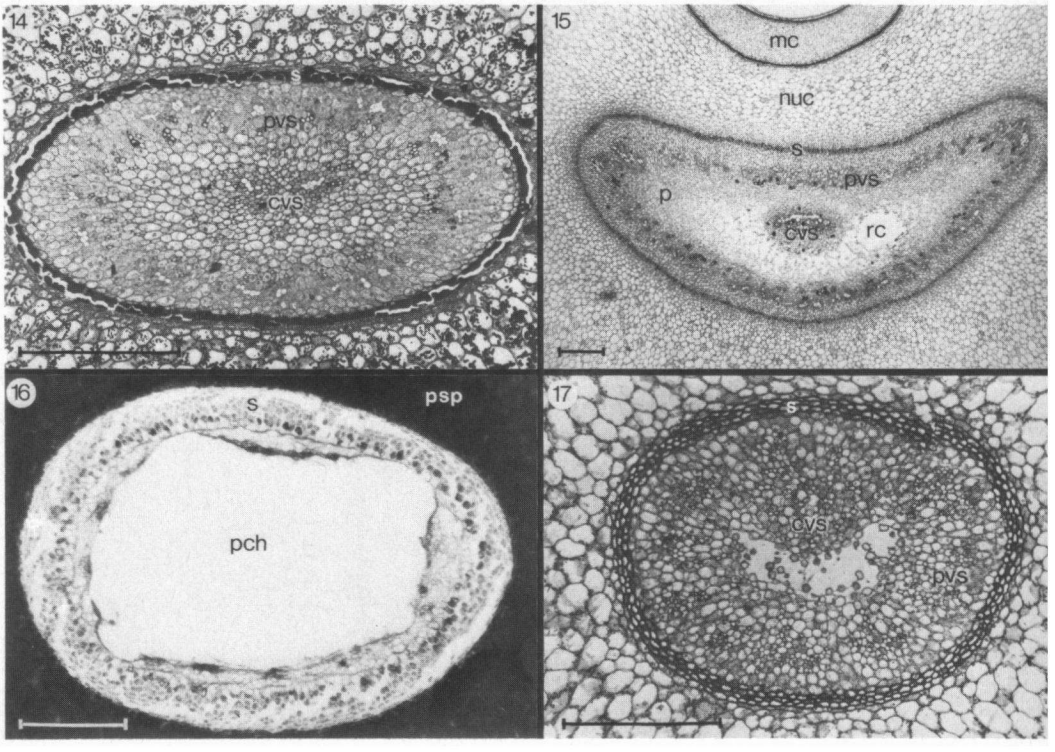

PLATE IV. Fig. 14: *Calathea picturata.* Cross section of the chalazal ingrowth of a half mature seed. A central (cvs) and a peripheral vascular system (pvs) are discernible. Between the two is a vacuolised parenchyma. The intrusion is surrounded by a sheath of tanniniferous cells (s).
Fig. 15: *Thalia dealbata.* Cross section of the basal unbranched part of the chalazal ingrowth of a developing seed. In the parenchyma (p) a rhexigenous cavity (rc) has developed.
mc = micropylar collar, nuc = nucellus.
Fig. 16: Cross section of one of the branches of the perisperm channel of *T. dealbata.* The perisperm channel (pch) arises by the degeneration of the vascular tissue and the parenchyma.
psp = perisperm.
Fig. 17: Chalazal ingrowth of a developing seed of *Ischnosiphon leucophaeus.*
In all figures: magnification bar represents 250 μm; the embryo sac is situated above.

a ring of small procambium strands originates which in turn gives rise to a second ring of (small) vascular bundles with the xylem at the outside *(fig. 14)*. Connections between the peripheral and the central vascular system are only present at the terminal part of the chalazal intrusion, the peripheral system ending blindly at the proximal side. In the small sheath cells ultimately some tannin-like substance is deposited; the adjoining nucellar cells form wall thickenings. The sheath passes gradually into the silicified endotesta.

During seed maturation the chalazal intrusion is cut off by the silification of the tissue in its narrow basal part. The intrusive tissue degenerates at the distal side of it, leaving some remains at the inner side of the tannin sheath and thus forming a hollow, closed-off perisperm channel.

b. *Thalia dealbata*

The ontogeny proceeds along the same lines as in *Calathea*. In the young ovule (before the campylotropous curvature begins) the procambial strand bifurcates immediately in front of the broad chalaza. In the course of development the bifurcation becomes surrounded by nucellar tissue. From the chalaza two protrusions grow out which bend forward along the embryo sac. As in *Calathea picturata* this intrusion consists of a vascular bundle (here situated excentrically, at the side of the embryo sac) and some parenchyma. It is surrounded by a sheath of small cells rich in cytoplasm. Intercellular spaces originate in the central parenchyma; the cells are longitudinally extended and remain in mutual contact by means of extensions until they become totally severed and a rhexigenous cavity is formed. A second, peripheral vascular bundle system originates which forms in the lateral arms of the chalazal intrusion a ring interrupted by the principal vascular strand and a continuous ring in the basal unpaired part of the intrusion *(fig. 15)*. At seed maturity the intrusion is cut off by tannin deposition and silification and subsequently degenerates (see *fig. 16)*.

c. Other species

Of *Maranta* spec., *Stromanthe stromanthoides, Ischnosiphon leucophaeus* and *I. puberulus* only the almost mature seed was studied. The chalazal intrusion is straight and distally ramified in the first two species, and straight and unbranched in *Ischnosiphon*. The anatomy of the intrusive structure does not differ essentially from the one described above (see *fig. 17: I. leucophaeus*).

3.4 Seed coat development

a. *Thalia dealbata*

The outer integument of *T. dealbata* initially consists of 6 – 7 cell layers. The cells of the inner- and outermost layers are subcubical, those of the middle layers are somewhat stretched longitudinally. By the time of fertilisation the cells of the inner and outer epidermal layers stretch while in the central layers there is mitotic activity *(fig. 18)*. In this way the integument is ultimately 10 – 15 cell layers thick. The innermost layer changes into a proper palisade layer *(fig. 19)* and silica bodies develop in the cell cavities. The walls become somewhat

crinkly in cross section *(fig. 20)* and start thickening; the lignified thickening layers are pitted and in the inner part (facing the inner integument) fill a considerable part of the lumen *(fig. 21)*. The middle layers consist of longitudinally stretched cells which become tanniniferous starting from the middle of the integument *(fig. 19)*; the cells lying more peripherally contain some starch grains. At a more mature stage the starch has dissappeared and some tannin is deposited in these cells. The middle layers eventually become somewhat compressed. Three zones can be distinguished, which differ in kind of tannin deposit and rate of obliteration *(fig. 21)*. The cells of the outer layer of the outer integument remain unthickened and stretch strongly in the radial direction, attaining a height of more than 100 μm *(fig. 20)*. At seed maturation this cell layer is squashed flat against the tannin cells *(fig. 21)*.

The inner integument is initially two cell layers thick, near the chalaza sometimes three, and consists of thin, elongated cells. During development it becomes somewhat obliterated, especially the outer layer *(fig. 20)*. Eventually its cells become sclerotic *(fig. 21)*; the wall thickenings show a positive reaction for lignin.

b. The other species

The seed coat ontogeny differs to some extent from that of *Thalia*. The inner integument also partakes in seed coat formation in *Stromanthe stromanthoides* and *Maranta* spec., but is more or less obliterated in *M. arundinacea, Calathea picturata, Ischnosiphon leucophaeus* and *I. puberulus*. There is no secondary increase in the middle layers of the outer integument. The innermost layer also forms crinkly, thickened walls, the cell lumen being taken up by a silica body. One or more tanniniferous layers originate and the cells laying outside these layers do not differentiate to an appreciable extent but are temporarily rich in starch *(fig. 27)*; the starch disappears again later *(fig. 22)* and the cells ultimately obliterate *(fig. 31)*.

3.5 Aril development

The aril is formed by periclinal divisions in the outer layer of the outer integument and the corresponding part of the raphe. Although it originates as a closed ring-shaped primordium, in some species its further development does not proceed at an equal rate around the ovule.

In *Calathea picturata* the greatest mitotic activity occurs at the sides of the raphe *(fig. 23, 28)*. The aril develops into two plicate lobes which are folded over on top of another at the raphal side of the seed *(fig. 11e, 29)*. It is white and consists of longitudinally much extended cells rich in starch in the almost mature seed, but, at complete seed maturity contain only oily inclusions. By the time of dehiscence the aril expands and unfolds presumably by an increase of the turgor. The pressure exerted by the aril makes the fruit dehisce along preformed zones of rupture in the dissepiments and in the pericarp midway over the seeds to form three valves and a central column, which releases the seeds which are subsequently scattered.

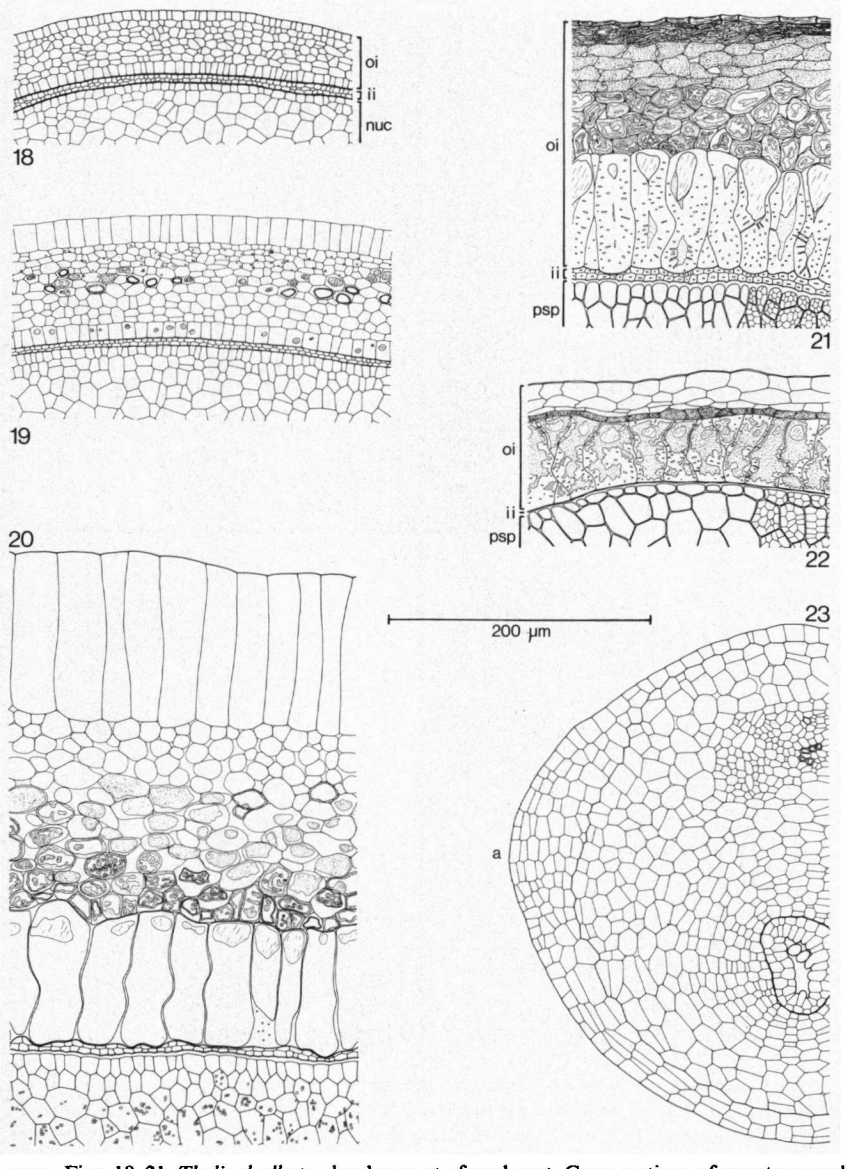

PLATE V. Figs. 18–21: *Thalia dealbata*, development of seed coat. Cross sections of a mature ovule, two developing seeds and a mature seed, respectively. ii = inner integument, nuc = nucellus, oi = outer integument, psp = perisperm.

Fig. 22: Cross-section of a nearly mature seed coat of *Calathea picturata*.

Fig. 23: *C. picturata*, cross section of a mature ovule showing aril primordium (a).

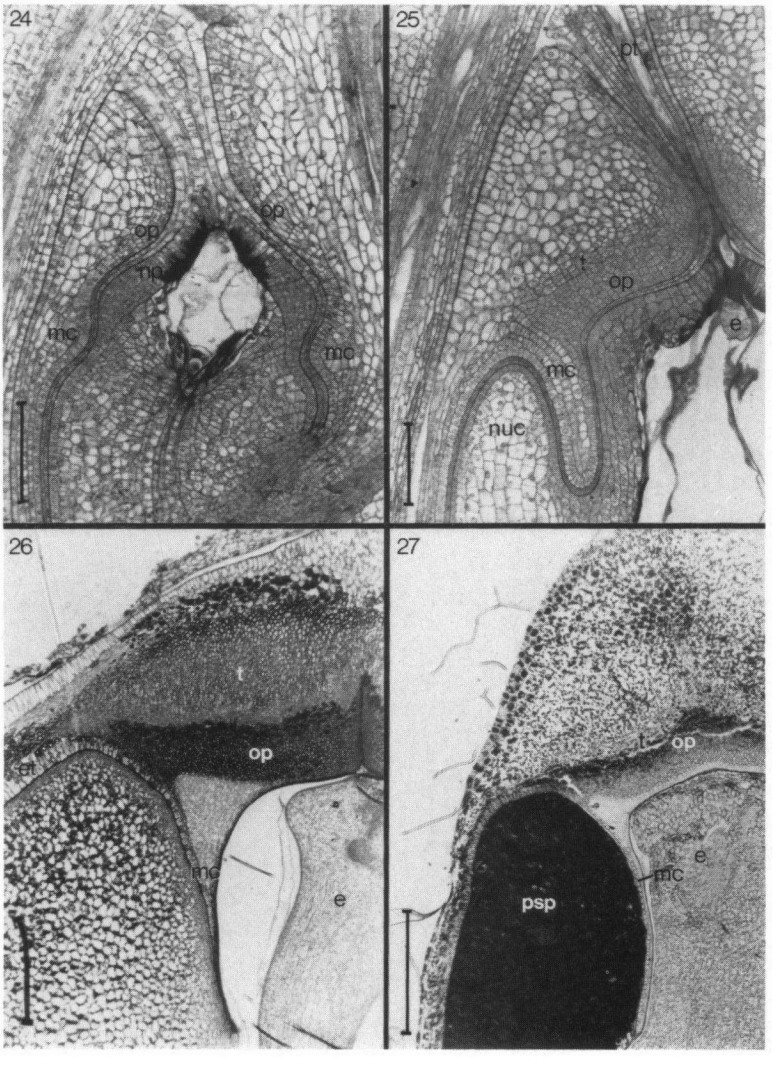

PLATE VI. Differentiation of the exostome area in *Calathea picturata* (Figs. 24, 25, 27) and *Thalia dealbata* (Fig. 26). The micropylar collar (mc) and sclerotic part of the operculum (op) are derived of the middle and inner layers of the exostome, respectively. The tannin cells (t) covering the operculum arise from the middle layers. Note the unthickened tissue at the inside of the collar (figs. 26, 27).
Magnification bar represents 100 μm in figs. 24, 25, and 500 μm in figs. 26, 27.
e = embryo, et = endotesta, np = nucellar pad, nuc = nucellus, pt = pollen tube.

In *Thalia dealbata,* which has indehiscent fruits, the aril is rudimentary and reduced, to two small swellings, one at each side of the raphe. In *Stromanthe stromanthoides* the aril is strongly developed around almost the whole of the exostome *(fig. 30)*. The mode of dehiscence of this species has not been observed.

3.6 Development of operculum and micropylar collar

Apart from the aril primordium in the outer layer of the exostome there are two other periclinally dividing cell groups, *viz.*, in its middle and its innermost layers, constituting the initials of the micropylar collar and the sclerotic part of the operculum, respectively. Both these structures originate as a complete ring, also at the raphal side *(fig. 24)*.

By mitotic activity in the middle layers and also owing to the growth of the nucellus the micropylar collar originates as an annular intrusion of the outer integument into the distal part of the nucellus *(fig. 25)*. This collar intrudes farther to an appreciable extent later, mainly by cell stretching. The collar is ultimately subcylindric in the more deeply situated part to widen towards the micropyle *(figs. 26, 27)*.

The cells of the inner layer of the exostome are originally rather small and form distinct rows (Fig. 25). This layer becomes several cell layers thick by repeated cell divisions, up to 25 layers near the micropyle in *Thalia dealbata* and even thicker in the part facing the micropylar collar. Also in this part, *i.e.*, above the primordium of the sclerotic operculum layers, mitotic activity starts in the middle layers *(fig. 25)*.

The cellular differentiation of the exostome begins with the formation of silica bodies and cell wall thickenings within the initiation zone of the operculum. This process initiates in the less deeply situated part facing the middle layers and proceeds in the direction of the nucellus. In the centre of the initiation disc, around the micropyle, all cells of the inner layer become sclerotic but towards the edge the walls of a gradually increasing number of cell layers remain unthickened, so that ultimately a disc of sclereids is formed, which towards the edge decreases in thickness *(figs. 26, 27)*. In the middle layers immediately above this disc, which have in the meantime become multi-layered after repeated periclinal cell divisions, tannin is deposited *(figs. 26, 27)*. In *Calathea picturata* the remaining distal portion of the outer integument develops into an aril, the cells first temporarily becoming starch-containing *(fig. 27)* but ultimately provided with oily inclusions. In *Thalia dealbata* this part differentiates in the same way as the remainder of the integument and becomes tanniniferous.

The cells of the outer layer of the micropylar collar gradually change from palisade cells with thickened walls and silica bodies as present in the endotesta to an unthickened epidermis with cubic cells in the deepest part of the collar. In *Calathea picturata* the palisade layer is divided into about isodiametric cells at the level of the disc of sclereid elements. The middle layers of the collar primarily remain unthickened but at a later stage also wall thickening and silica deposition takes place in the area adjoining the sclerotic part of the operculum. In the deeper part of the collar some tannin is formed in the middle layers whereas

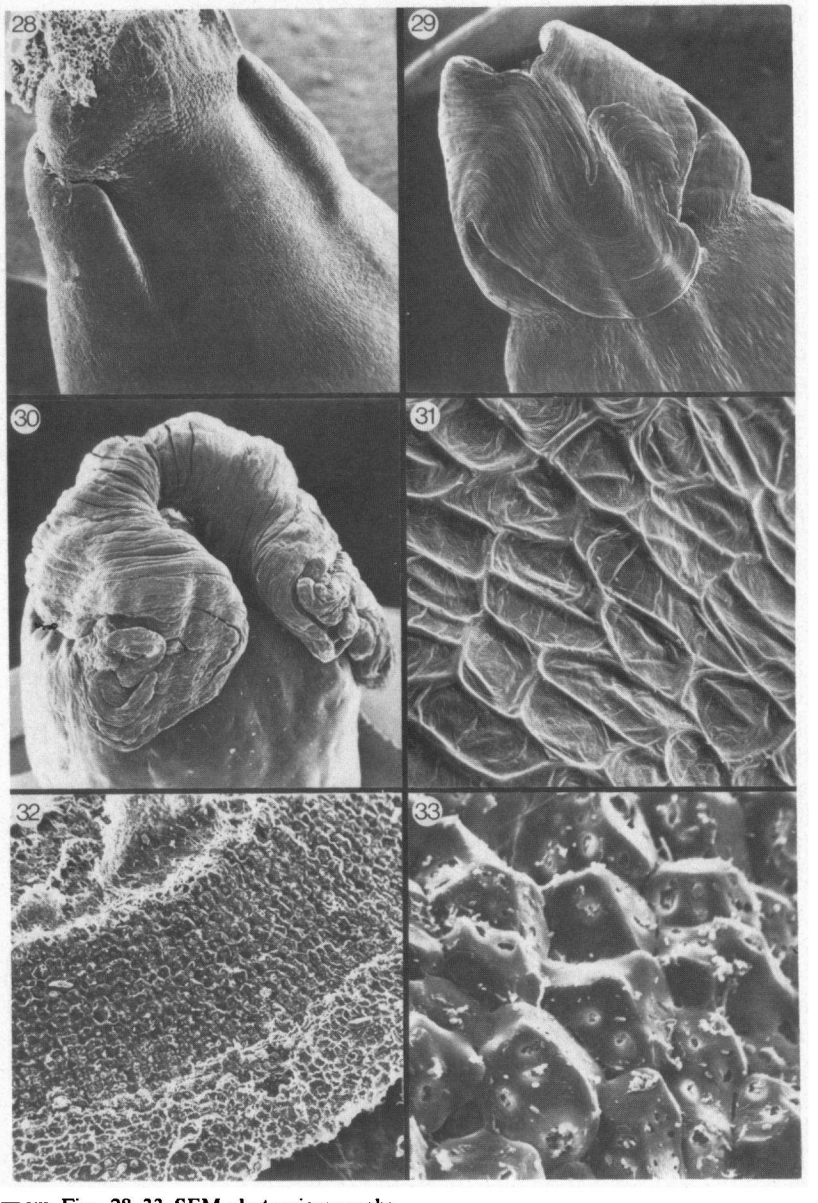

PLATE VII. Figs. 28–33: SEM photomicrographs.
Figs. 28, 29: *Calathea picturata*, development of aril: developing (50 ×) and nearly mature seed (12 ×), respectively.
Fig. 30: *Stromanthe stromanthoides*, aril (10 ×).
Fig. 31: Surface view of a mature seed coat of *C. picturata* (400 ×).
Fig. 32, 33: Face of rupturing of an operculum of *C. picturata* 100 × and 1000 ×, respectively.

the inner side (facing the embryo sac) remains parenchymatic. The sclerotic part of the operculum thus becomes fused with the endotesta, so that the interior of the seed is protected by a completely closed coat of silicified sclerotic tissue surrounded by a tanniniferous layer.

4. DISCUSSION

The Marantaceae have a dermally initiated inner, and a subdermally initiated outer integument. Integuments of subdermal derivation had not previously been recorded in monocotyledons. In dicotyledons such integuments are considered to be primitive (BOUMAN & CALIS 1977). From the viewpoint of comparative morphology (especially as regards the androecial structure and the reduction of the ovary) the Marantaceae are the terminal members of an evolutionary lineage within the Zingiberales and constitute one of the most advanced groups among the Liliatae (SCHUMANN 1902). The vegetative anatomy does not point at a primitive status of this family either (TOMLINSON 1962). It does not necessarily follow, however, that the Marantaceae are advanced in all their characters because they exhibit a number of derived features. A possible explanation is the incidence of heterobathmy, *i.e.*, the occurrence of one or a few primitive characters next to many advanced ones. This supposition may be put to the test by a comparative study of integument initiation in the other families of the Scitamineae, especially in the Strelitziaceae s.s., supposed to represent the most primitive family of the order (TOMLINSON 1962). It had already been established that in Cannaceae (HUMPHREY 1896) and in Costaceae (GROOTJEN & BOUMAN 1981) both integuments are of dermal origin, and since apparently both modes of integument initiation occur in the Zingiberales, an inquiry into the distribution of this feature may conceivably yield some indications regarding the relationships within the order.

The placental region of the Marantaceae is originally dizonate, *i.e.*, consists of a periclinally dividing corpus surrounded by an only anticlinally dividing tunica layer. At a later ontogenetic stage the primordium becomes trizonate because two tunica layers are present owing to the reorganisation of the corpus into a second, subdermal tunica layer and the periclinally dividing inner layers. Such a "reshuffling" of layers also takes place during the development of the exostome. As is also the case in the other families of the Zingiberales (MAURITZON 1936, GROOTJEN & BOUMAN 1981), the aril, the sclerotic part of the operculum and the micropylar collar are derived from, respectively, the outer, inner, and the middle layers of the exostome. Needless to say the outer and inner layers are always of dermal derivation, but the middle layers of the exostome and consequently the micropylar collar, may have different origins. The collar is initiated as a complete ring which consists of a tegumentary part and a small sector contributed by the raphe. In *Pleiostachya pruinosa* the tegumentary part is subdermal but the raphal part dermal because at this side of the ovule a pluri-layered dermal mass of tissue has formed; in *Thalia dealbata* the whole collar is of subdermal derivation because the dermal proliferation in the raphal region does

not extend as far as the site of initiation of the collar; and in Costaceae, finally, the tegumentary contribution is of dermal, and the raphal one of subdermal origin (GROOTJEN & BOUMAN 1981). Undoubtedly the micropylar collar is homologous in these three cases and a "reshuffling" must have occurred in the exostome which independently of a primarily dermal or subdermal initiation becomes reorganised into an inner, a middle and an outer layer.

A characteristic feature of the marantaceous seed is the perisperm channel, a structure unique among all angiosperms. By a complicated interaction of chalazal and nucellar differential growth chalazal tissue comes to lie within the nucellus. This vascular tissue is entirely of chalazal origin and not, as HUMPHREY (1896) suggested, derived from nucellar tissue. The hollow perisperm channel originates during seed maturation by the degeneration of the cells of the chalazal intrusion. SCHACHNER (1924) suggested three possible functions of the intrusive tissue, *viz.*, to supply nutrients and water, to facilitate water uptake during germination, and exchange of gases with the outside world. The last two possibilities appear to be most improbable because the intrusion becomes closed off, something Schachner overlooked. The position of the principal vascular strand, oriented towards the embryo sac, points to the first (translocation) function. By the ingrowth the distance to be bridged is much shortened and the providing area much enlarged, to which the campylotropy also contributes.

The principal mechanical layer of the seed coat of the Marantaceae is derived from the innermost layer of the outer integument and develops into a markedly silicified endotesta. Out of the middle layers of the integument, sometimes increasing in number by secondary multiplication, a tanniniferous layer of one to several cell layers thick develops which lies immediately against the endotesta and is reponsible for the colour of the seed. The remainder of the outer integument, *i.e.*, the cells of the outermost layer, which may stretch radially to an appreciable extent, and sometimes also the outer middle layers, remains unthickened and is ultimately squashed flat and obliterates. The participation of the inner integument (thin elongated sclereids) in the formation of the seed coat in some Marantaceae is an unique feature among the Zingiberales. The presence of an endotesta is rather common and has been reported to occur in Strelitziaceae *(Ravenala)*, Zingiberaceae and Costaceae (NETOLITZKY 1926).

The occurrence of arilli, opercula and micropylar collars within the Zingiberales has been discussed elsewhere (GROOTJEN & BOUMAN 1981). When the aril is well-developed it has a function associated with fruit dehiscence; it is, accordingly, rudimentary in indehiscent fruits. The presence of oil drops in the aril of *Calathea picturata* points, in addition, to an adaptation to myrmecochory, see HORVITZ & BEATTIE (1980). The absence or the unequal development of the aril around the exostome in some Marantaceae is a secondary development, as is evident from the fact that primarily always an initiation takes place by periclinal divisions all around the exostome. Moreover, sometimes the adaptive significance of indehiscence is demonstrable: *Thalia dealbata*, a helophyte found in marshy habitats, even has a manifest adaptation to hydrochory in that between the seed and the pericarp there is a gasfilled space rendering the fruit

capable of floating on the water surface. The wax-covered water-repellent bracts attached to the fruit also contribute to this property.

Around the micropyle the operculum and the micropylar collar are formed, the latter is initiated in the middle tegumentary layers, the cells of the innermost layer only dividing anticlinally. The collar ultimately forms, by silification of the outer layer (facing the perisperm) a sclerotic ring which partly surrounds the embryo. The operculum originates more distally and consists mainly of numerous layers of silicified sclereids derived from the innermost exostome layer covered by several layers of tannin cells derived from the middle exostome layers. Apart from additional mitotic activity and a secondary multiplication of layers the determination of the cells, *viz.*, innermost layer becoming silicified sclereids, and middle layers becoming tannin cells, is in the greater part of the exostome very much the same as in the remainder of the integument.

However, in two places this determination pattern deviates: firstly, in the micropylar collar between the sclerotic part of the operculum and the endotesta, where in cells derived from the middle tegumentary layers silification takes place; and secondly, at the inside of the collar and the adjacent part of the initiation zone of the operculum within the innermost exostome layers where the cells remain parenchymatic. This renders the sclerotic part of the operculum the shape of a disc tapering all around towards the outer rim. During germination the pressure exerted by the swelling embryo will be directed against the operculum through the micropylar collar and the former ruptures in the weakest (most tenuous) place, *i.e.*, in the region of the collar. The plane of rupturing is parallel with, and a few cell layers away from the endotesta and takes place along the middle lamellae *(figs. 32, 33)*. This is made possible by the widening of the collar at that site: the sclerotic part of the operculum is not situated in the collar but is more overlying.

The preformation of the site of rupturing in Marantaceae is less differentiated than it is in Costaceae, where within the micropylar collar a severing layer of thin-walled cells is present (GROOTJEN & BOUMAN 1981).

The fusion of operculum and endotesta provides a firm protection of the seed; the associated difficulties during germination are (partly) compensated by the presence of an unthickened tissue at the inside of the collar and in the adjacent area. As could be shown experimentally, the germination in Marantaceae is a lengthy and staggered process: of 16 fresh seeds of *Calathea picturata* the first sprouted after two months and after eight months only nine had germinated.

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REFERENCES

ANDERSSON, L. (1981): The neotropical genera of Marantaceae. Circumscription and relationships. *Nord. J. Bot.* **1**: 218–245.

BOUMAN, F. & J. J. M. CALIS (1977): Integumentary shifting – a third way to unitegmy. *Ber. Deutsch. Bot. Ges.* **90**: 15–28.

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

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

EICHLER, A. W. (1884): *Beiträge zur Morphologie und Systematik der Marantaceen.* Berlin.

GRIS, A. (1859): Observations sur la fleur des Marantées. *Ann. Sci. Nat. Bot. 4. Sér.* **12**: 193–219.

— (1860): Note sur l'origine et le mode de formation des canaux perispermiques dans la graine des Marantées. *Ann. Sci. Nat. Bot. 4. Sér.* **13**: 97–102.

GROOTJEN, C. J. & F. BOUMAN (1981): Development of ovule and seed in Costus cuspidatus (Zingiberaceae), with special reference to the formation of the operculum. *Bot. J. Linn. Soc.* **83**: 27–39.

HORVITZ, C. C. & A. J. BEATTIE (1980): Ant dispersal of Calathea (Marantaceae) seeds by carnivorous ponerines (Formicidae) in a tropical rain forest. *Amer. J. Bot.* **67**: 321–326.

HUMPHREY, J. E. (1896): The development of the seed in the Scitamineae. *Ann. Bot.* **10**: 1–40.

MAURITZON, J. (1936): Samenbau und Embryologie einiger Scitamineen. *Acta Univ. Lund* **31**: 1–31.

MÜLLER, F. (1883): Einige Nachträge zu Hildebrand's Buche: Die Verbreitungsmittel der Pflanzen. *Kosmos* **7**: 275–283.

NEES VON ESENBECK, C. G. (1831): Ueber die Gattungen Maranta und Thalia. *Linnaea* **6**: 303–342.

NETOLITZKY, F. (1926): *Anatomie der Angiospermen-Samen.* Berlin.

RODE, W. W. (1913): *Schutzeinrichtung von Fruchten und Samen gegen Einwirkung fliessenden Meerwassers.* Diss. Göttingen.

SCHACHNER, J. (1924): Beiträge zur Kenntnis der Blüten- und Samenentwicklung der Scitamineen. *Flora* **117**: 16–40.

SCHUMANN, K. (1902): Marantaceae, in: A. ENGLER: *Das Pflanzenreich* **IV 48.** Leipzig.

TOMLINSON, P. B. (1962): Phylogeny of the Scitamineae – morphological and anatomical considerations. *Evolution* **16**: 192–213.

VENKATASWARALU, V. (1937): A note on the development of the embryo sac in Phrynium capitatum W.. *J. Indian Bot. Soc.* **16**: 95–98.