The genus *Eugenia* (Myrtaceae) in southern Africa: Ontogeny and taxonomic value of the seed

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Eugenia L. in southern Africa constitutes two coordinate groups of species (groups X and Y). Each group is characterized by a particular type of seed (types X and Y respectively). This study concerns the ontogeny of both seed types. Results are compared with the literature to evaluate its taxonomic significance.

In both groups the ovules are hemi-campylotropous, occasionally tending to be ana-campylotropous, sessile or sub-sessile, bitegmic and crassinucellate. Usually only one ovule per ovary matures into an overgrown seed. Abortive ovules are transformed into ovulodes.

Ovules in seed type X become amphitropous resulting in sub-reniform or oblong-globose seed. A short funicle is discernible; the hilum is not extended. The testa develops from the outer integument and is relatively thin (0,1 – 0,5 mm), not multiplicative and tends to be exotestal. Two areolae pervaded by vascular strands are present. Secretory cavities develop in the cotyledons. Starch, occasionally with unidentified spherical bodies, is the main storage product. Abundant endosperm is formed.

Seed type Y is globose, pachychalazal and sessile with an extended hilum. The testa is relatively thick (0,5 – 1,0 mm), multiplicative, mesotestal and pervaded by vascular strands. Secretory cavities are absent from the cotyledons. Starch is the only storage product. Relatively little endosperm is formed.

Generic rank is proposed for both groups. Group X is treated as congeneric with *Eugenia s. str.* whereas group Y probably represents a new generic segregate.

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Eugenia L. in suidelike Afrika word deur twee newegeskikte spesiegroepe (groepe X en Y) verteenwoordig. Elke groep word deur 'n besondere saadtipe gekenmerk (tipes X en Y onderskeidelik). Hierdie ondersoek handel oor die ontogenie van beide saadtipes. Die resultate word met literatuurgegewens vergelyk ten einde die taksonomiese betekenis daarvan te evalueer.

Saadknoppe van beide groepe is hemi-kampilotropies (soms geneig om ana-kampilotropies te wees), sittend of half-sittend, bitegmies en krassinusellêr. Gewoonlik ontwikkel slegs een saadknop per vrugbeginsel in 'n uitermate vergrote saad. Die oorblywende saadknoppe aborteer en is blywend.

In die geval van saadtipe X word die saadknoppe amfitropies met die gevolg dat die saad halfniervormig of langwerpig-rond is. Die funikulus is baie kort en daar is geen vergroting van die hilum nie. Die relatief dun (0,1 – 0,5 mm) testa ontwikkel uit die buitenste integument, is nie veellagig nie en neig om eksotestaal te wees. Twee areole deurtrek met vaatstringe is teenwoordig. Sekreetholtes ontwikkel in die saadlobbe. Stysel, soms tesame met ongeïdentifiseerde bolvormige strukture, is die hoofbergingsproduk. Baie endosperm word gevorm.

Tipe Y sade is bolrond, pagichalasaal en sittend met 'n vergrote hilum. Die relatief dik (0,5 – 1,0 mm) testa is veellagig, mesotestaal en deurtrek met vaatstringe. Sekreetholtes is afwesig in die saadlobbe. Stysel is die enigste bergingsproduk. Relatief min endosperm word gevorm.

Genusrang word vir beide groepe voorgestel. Groep X word beskou as kongeneries met *Eugenia s. str.*, terwyl groep Y waarskynlik 'n nuwe genus verteenwoordig.

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1. Introduction

On the basis of anatomical characters, Van Wyk (1978) proposed that the southern African species of *Eugenia* L. constitute a heterogeneous assemblage of two coordinate groups of species (designated groups X and Y). Strong support for the proposed grouping was subsequently obtained from the morphology of the seed (Van Wyk 1980). Two different types of seed were briefly described in the latter preliminary note. Little attempt was, however, made to name the various parts of the seed or to explain the differences observed. In the present paper we shall, for convenience, refer to seed type X or Y according to the group of species it characterizes.

In Myrtaceae, and in particular the tribe Myrteae, considerable taxonomic value has traditionally been attributed to seed characters (see 4.1 for a discussion and references). We therefore believe that the morphology of the seed may be crucial in the eventual assessment of the formal taxonomic status of groups X and Y.

This paper is complementary to Van Wyk (1980) and deals with aspects of the ontogeny of seed types X and Y. The principal aim of the study is to gain a better understanding of seed structure in order to explain the various structural features and to evaluate their taxonomic significance. Finally, we shall attempt to propose a formal taxonomic rank for the two groups of species.

2. Material and Methods

Van Wyk (1980) did not report significant interspecific variation in the morphology of mature seeds within groups X and Y. Consequently it was assumed that the development of the seed is the same in all the species within each group. The ontogeny of seed type X was studied in detail in *E. simii* Duemmer and that of type Y in *E. zeyheri* Harv. In addition, stages in the seed ontogeny of 11 other southern African species of *Eugenia* were studied to test the above-mentioned assumption. A list of the examined species and selected voucher specimens is provided in Table 1. All collection numbers are those of the first author and voucher specimens are deposited in the H.G.W.J. Schweickerdt Herbarium (PRU).

Fresh flowers and fruits at various stages of development were fixed in FAA. For a light microscopical study, material was embedded according to standard methods in either Paraplast paraffin wax or glycol methacrylate (GMA). Sections were stained with safranin O-fast green (Sass 1958) and periodic acid/Schiff's (PAS) reaction-toluidine blue (Feder & O'Brien 1968), respectively.

Whole ovules were partly cleared in Herr's (1971) clearing

Table 1 Species of *Eugenia* studied and selected voucher specimens

Group	Species	Collection numbers		
X	*E. capensis* (Eckl. & Zeyh.) Sond.	994;	1546;	2619.
X	*E. natalitia* Sond.	1318;	1372;	4854.
X	*E. simii* Duemmer	1269;	1270;	3296.
X	*E. umtamvunensis* Van Wyk	3283;	3631;	5132.
Y	*E. albanensis* Sond.	3140;	3142;	5346.
Y	*E. erythrophylla* Strey	1313;	4336;	5028.
Y	*E. verdoorniae* Van Wyk	1614;	3280;	3284.
Y	*E. woodii* Duemmer	4874;	4877;	5440.
Y	*E. zeyheri* Harv.	2131;	2180;	3134.
Y	*E. zuluensis* Duemmer	1241;	2661;	3291.
Y	*E.* sp. A.	1287;	3269;	5079.
Y	*E.* sp. B.	3269;	4239.	
Y	*E.* sp. C.	1303;	3297;	5099.

fluid and examined with bright field and polarized optics. Following standard procedures material was also studied with the scanning electron microscope (SEM) after critical point drying with liquid CO_2.

Ovular structure was studied at anthesis. This is the stage during which fertilization presumably occurs and development of the seed commences. Embryo development has not been followed in detail. Unless otherwise indicated, the descriptive terminonology with regard to seed structure proposed by Corner (1976) is used. Descriptors used to indicate abundance and frequency are based on those proposed by Schmid (1982).

3. Observations

3.1 Ovule structure and placentation

The inferior ovary is nearly always bilocular — rarely trilocular or unilocular. The locules alternate with the pair of bracteoles and inner calyx lobes, hence are opposite to the outer calyx lobes. A conspicuous compitum (Carr & Carr 1961) in the form of a pore or vertical slit is present in the top median part of the septum.

Placentation is axile. In each locule a disc shaped or subpeltate placenta (Figure 8) occurs in the centre or upper third of the septum — usually directly below the compitum (Figure 1). Abundant deposits of tanniniferous substances rendered the fixed placental tissue dark brown or black in specimens of *Eugenia albanensis* (Figure 2). The main ovular vascular supply is transeptal.

The number of ovules per locule is usually two to four, rarely one or five. At anthesis the locule is virtually filled by the collateral ovules which are ventral hypotropous (McLean & Ivimey-Cook 1956), rarely heterotropous (Warming 1913 according to Björnstad 1970) (Figure 1). At this stage the shape of the ovules in both groups of species can probably best be described as hemi-campylotropous, occasionally tending to be ana-campylotropous (Bocquet & Bersier 1960) (Figures 1 – 4, 11A & 12A). They are usually sessile (Figures 2 & 8), occasionally with a very short funicle, especially in species belonging to group X (Figures 3, 4 & 7).

Ovules of all the species are bitegmic and crassinucellate (Figures 1 & 2). The micropyle is usually formed by both outer and inner integuments, occasionally by the inner integument only (Figure 5). The latter condition was especially marked in some specimens of *E. woodii*. In surface view the exostome is circular, triangular or slit-like (Figure 7). No clearly discernible hypostase (Dahlgren 1940) has been observed although the nucellar and chalazal cells near the base of the embryo sac were occasionally slightly smaller, flattened or less transparent in partly cleared ovules (Figure 4).

Over the greater part of its free length, the outer integument is four to six and the inner integument nearly always two (rarely locally three) cell layers thick (Figure 2). Distally both integuments thicken owing to an enlargement of cells and a slight increase in the number of cell layers (Figures 2, 4 & 5). The inner integument is rather inconspicuous and could be overlooked, particularly in wax embedded ovules not sectioned in the median-longitudinal plane. No air gaps occur between the two integuments, nor between the inner integument and the nucellus.

In the vicinity of the micropyle tanniniferous deposits are often present in the outer epidermal cells of the outer integument (Figure 1). Exceptionally large druse crystals presumably of calcium oxalate have been observed in the cleared ovules of a specimen of *E. capensis* (Figures 3 & 4). These crystals were apparently deposited in the nucellus (embryo sac?). Smaller druse crystals are usually abundant in the cells of the ovary wall, placenta and funicle (when present), rarely in the integuments.

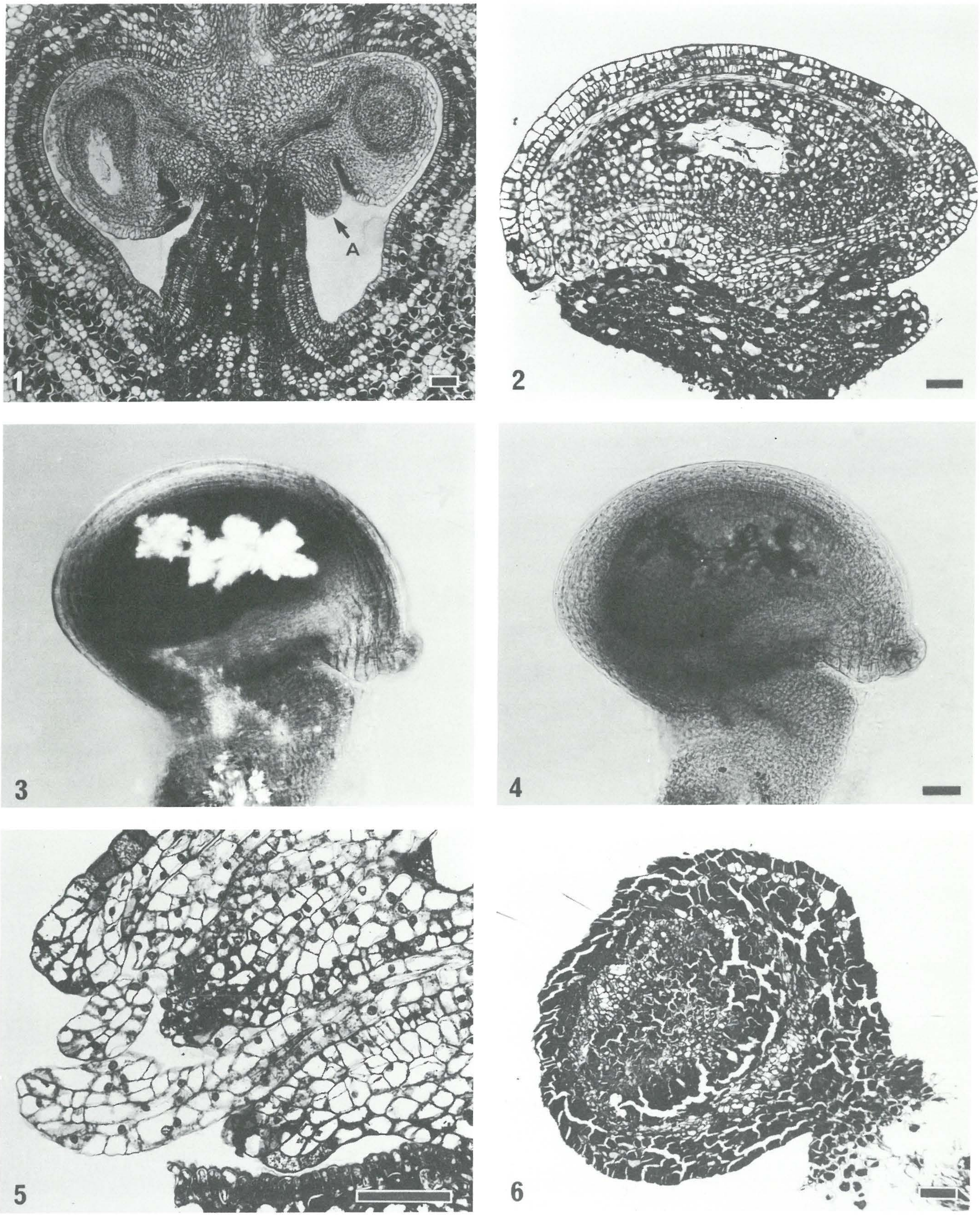
Usually only one (rarely two to three) ovule per ovary matures into a seed. The abortive ovules are transformed into ovulodes (see 3.4). Our observations indicate that the salient features of seed development are similar in all the species of a single group. This supports our initial assumption. Despite some mutual features though, the ontogeny of seed types X (Figures 9 & 11) and Y (Figures 10 & 12) is quite different and is therefore described separately (see 3.2 and 3.3 respectively). These descriptions include the entire range of variability for all the particular specimens.

3.2 Ontogeny of seed type X

Seed development (Figure 11A – D) starts with a rapid enlargement of the ovule. This results in a considerable displacement of the septum and pressure against the wall of the pericarp. The seed is overgrown (Corner 1976) and its position and shape is usually reflected by that of the developing fruit.

Very soon after the initiation of seed development, the ovule becomes amphitropous (see below) and a very short funicle becomes clearly distinguishable, even if the ovules were initially apparently sessile (Figure 11B). During development the amphitropous shape is accentuated (less so in *E. capensis*) by a rapid expansion of the dorsal side of the seed. The shape of the mature seed is therefore more or less reniform, except in *E. capensis* where it tends to be oblong-globose (Figures 9A & 11D). There is also a slight elongation but virtually no appreciable thickening of the funicle. Eventually the funicle becomes laterally slightly flattened. It leaves a linear-elliptic hilum on the ventral side of the mature seed (Figure 9A). The micropyle closes at an early stage and is not clearly discernible in the mature seed. The pericarp remains free from the testa except in *E. capensis* where the testa tends to adhere to the pericarp from an early stage of development.

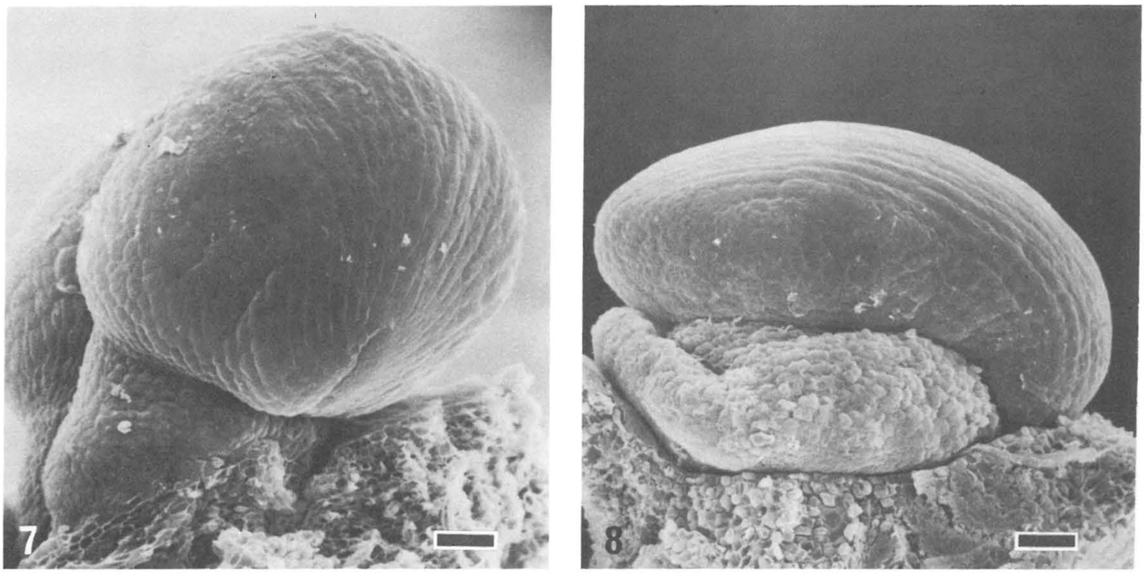
The relatively thin, leathery or rather brittle (when dried out) testa develops from the outer integument. At an early stage of development the inner integument is crushed although vestiges of its thicker distal part persist somewhat longer in the micropylar region (Figures 11B & 15). Limited divisions of the mesophyll cells result in a slight increase in the thickness of the outer integument (Figure 14). The outer epidermal cells enlarge and become more or less radially elongated in transverse section. Tanniniferous substances are deposited abun-



Figures 1 – 6 Placentation and ovule morphology. 1. *E. capensis* (*Van Wyk* 2619), longitudinal section of ovary showing two ovules and placenta (A). 2. *E. albanensis* (*Van Wyk* 3140), longitudinal section of ovule attached to a highly tanniniferous placenta. 3 & 4. *E. capensis* (*Van Wyk* 2619), cleared ovule showing large druse crystals under polarized light (3) — note micropylar thickening of the integument. 5. *E. woodii* (*Van Wyk* 4874), longitudinal section of micropylar region of ovule with the inner integument forming the exostome. 6. *E. natalitia* (*Van Wyk* 4854), transverse section of an ovulode. Scale line = 50 μm.

dantly (less so in *E. capensis* — Figure 16) in most of the epidermal and mesophyll cells.

The epidermal layer of the testa (Figures 20 – 22) develops from the outer epidermis of the integument. During expansion of the seed the outer epidermal cells increase by means of mainly anticlinal divisions. Very limited periclinal divisions



Figures 7 & 8 SEM micrographs of ovules. 7. *E. capensis* (*Van Wyk* 2586) showing slit-like micropyle and short funicle. 8. *E. albanensis* (*Van Wyk* 3140) — note disc-shaped placenta and sessile ovule. Scale line = 50 μm.

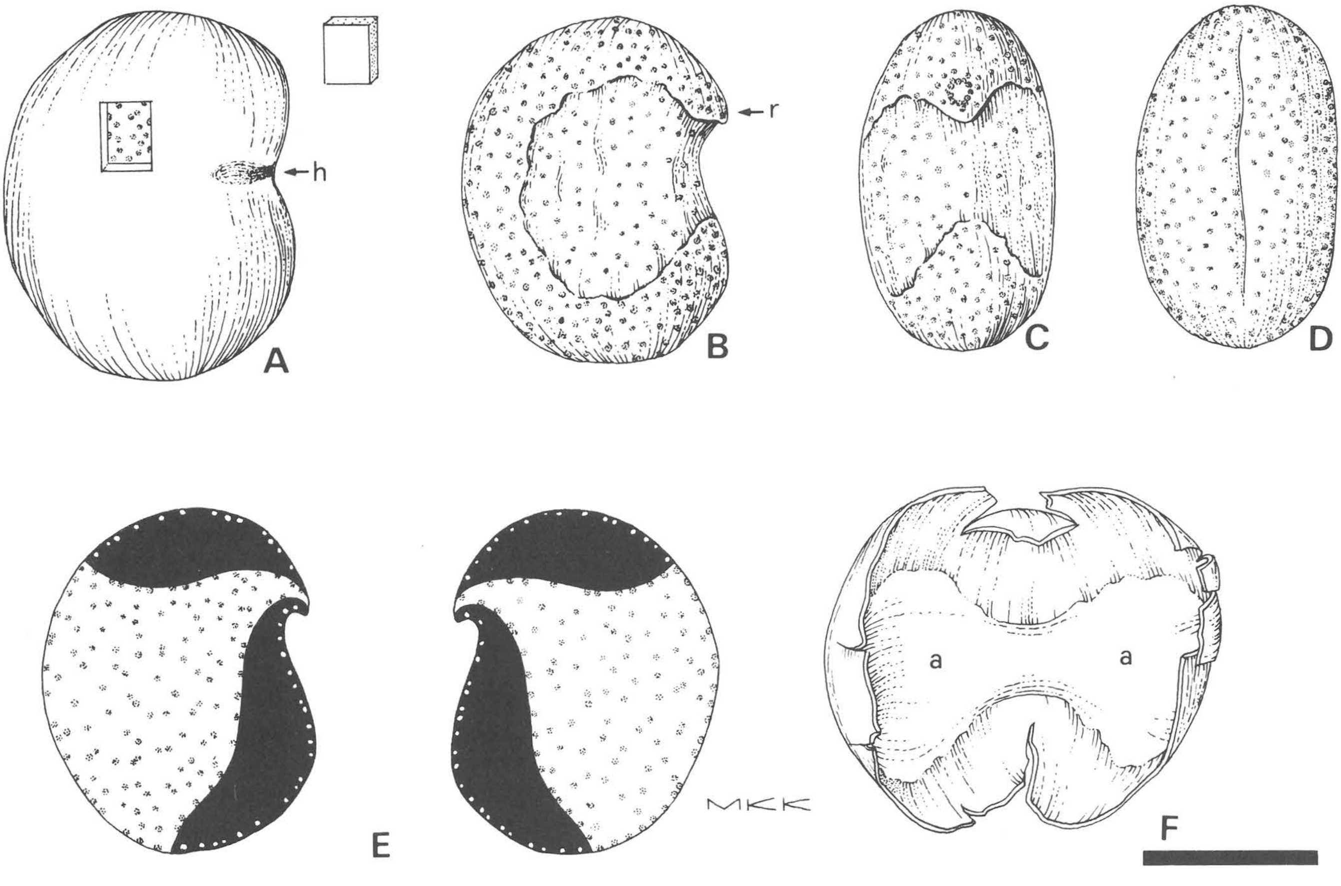


Figure 9A – F Morphology of seed type X. Mature seed of *E. natalitia* (*Van Wyk* 4854). A. Seed with part of testa removed showing surface of embryo beneath. B. Lateral view of glandular punctate embryo showing the impression left by the areolae. C. Ventral view of embryo showing spot of densely arranged secretory cavities on radicular protuberance. D. Dorsal view of embryo showing the short line of separation between the two cotyledons. E. Split open embryo showing region of fusion (black) between cotyledons. F. Split open testa showing the areolae. (a – areolae; h – hilum; r – radicular protuberance) Scale line = 5 mm. {Reproduced with additions from Van Wyk (1980).}

occur. The cells also elongate periclinally and become fibre-like. In the developing testa the walls of these cells are the first to thicken and become lignified. The anticlinal, inner periclinal and occasionally outer periclinal walls become conspicuously thicker and lignified (less so in *E. capensis*). The resultant fibre-like sclereids have numerous bordered pits and are usually somewhat flattened radially, probably owing to pressure exerted by cell enlargement and the increase in wall thickness. The epidermis of the mature testa is well differentiated (less so in *E. capensis*) and in transverse section resembles a palisade of radially elongated macrosclereids with heavily pitted cell walls (Figures 20 & 22). However, the outer periclinal walls

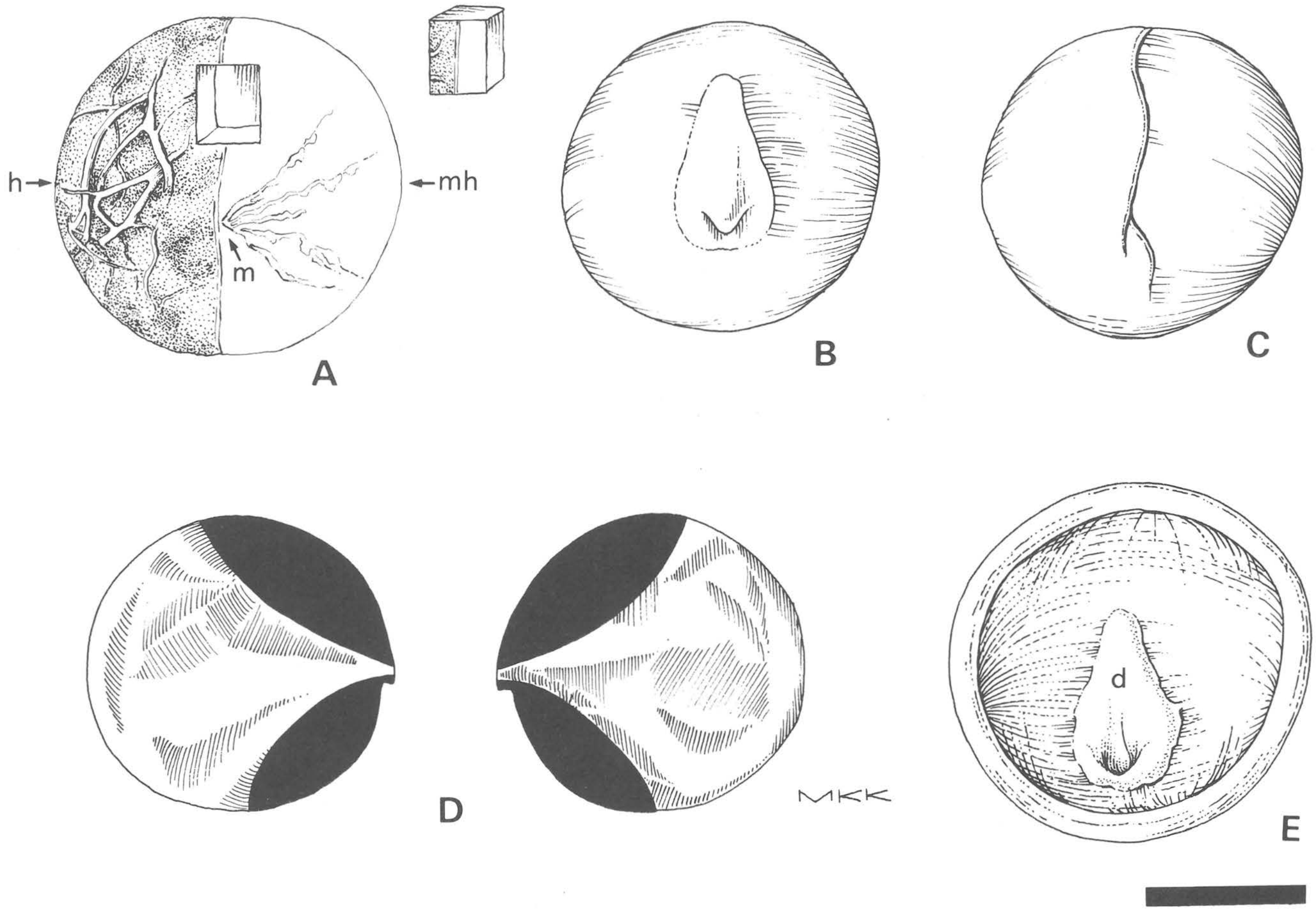


Figure 10A – E Morphology of seed type Y. Mature seed of *E. zeyheri* (*Van Wyk* 3134). A. Seed with part of testa removed showing embryo beneath — note remains of placental tissue (vascular bundles) on hilar hemisphere and wedge-shaped patch of mottled testa (reflecting the position of the depression on the inner surface of the testa) on micropylar hemisphere. B. Embryo with short radicular protuberance surrounded by a raised area of tissue matching the shape of the depression on the testa — note lack of secretory cavities. C. Embryo with branched line of separation between the two cotyledons. D. Split open embryo showing irregular inner surface of cotyledons and region of fusion (black). E. Half of testa showing the more lightly coloured (often mottled) depression on the inner surface. (d – depression; h – hilar hemisphere; m – micropyle; mh – micropylar hemisphere) Scale line = 5 mm. {Reproduced with changes and additions from Van Wyk (1980).}

often remain unlignified.

The mesotesta develops from the mesophyll and apparently inner epidermis of the integument. The latter becomes obscured by the remains of the crushed inner integument and nucellus. After a slight increase in the number of cell layers the mesophyll cells elongate mainly periclinally and become fibre-like. This is followed by the thickening and lignification of the cell walls. Owing to intrusive growth during cell elongation, the mature mesotesta consists of haphazardly arranged fibre-like sclereids (Figures 20 & 21). Cell walls are abundantly pitted (bordered pits).

There is a definite tendency for the outer epidermal layer to function as the main mechanical tissue in the mature testa (less so in *E. capensis*, and the areolar regions). This was without doubt the case in a specimen of *E. natalitia* in which many of the mesophyll cells remained thin walled and unlignified (Figure 22). Hence seed type X tends to be exotestal.

When viewed from the inside two more darkly coloured areas are visible on the lateral sides of the testa (Figure 9F). These areas are ventrally connected by a narrow isthmus (see Van Wyk 1980). We shall refer to these areas (which are usually not clearly visible from the outside) as the areolae. The areolae are already visible at a very early stage of development. Their appearance seems to coincide with the amphitropous curvature of the ovule. The development of the areolae will now be considered in more detail (Figure 11C & 13).

In the hilar region of the very young seed, proliferation of the tissue of the outer integument, funicle and mainly chalaza, results in a ventral hump of tissue bulging against the nucellus. This tissue is traversed by vascular strands derived from the funicular bundle. It is suggested that lateral extensions of the vascular strands to the sides of the seed lead to the appearance of tracheary elements in the deeper layers of the outer integument. An alternative interpretation is that the areolar regions of the testa develop from the chalaza only, without any involvement of the free part of the outer integument. Concurrently there is an increase in the number of cell layers and deposition of tanniniferous substances in this part of the mesophyll. The testa of the areolar region, therefore, differs from that of the remainder of the seed in being thicker, more darkly coloured and abundantly pervaded by vascular tissue. In addition the remains of the nucellus and probably crushed inner integument are relatively thick and strongly tanniniferous in this region (Figures 11C, 13 & 16). The abundant deposits of tanniniferous substances are responsible for the dark brown colour of the areolae.

The young embryo is located in the micropylar region of the seed (Figures 11B & 15). The initial increase in size of the embryo is slow and only speeds up after considerable enlargement of the seed has taken place. The shape of the mature embryo is consequently determined by that of the 'seed'. A mature embryo (Figure 9B – E) consists of two partly fused

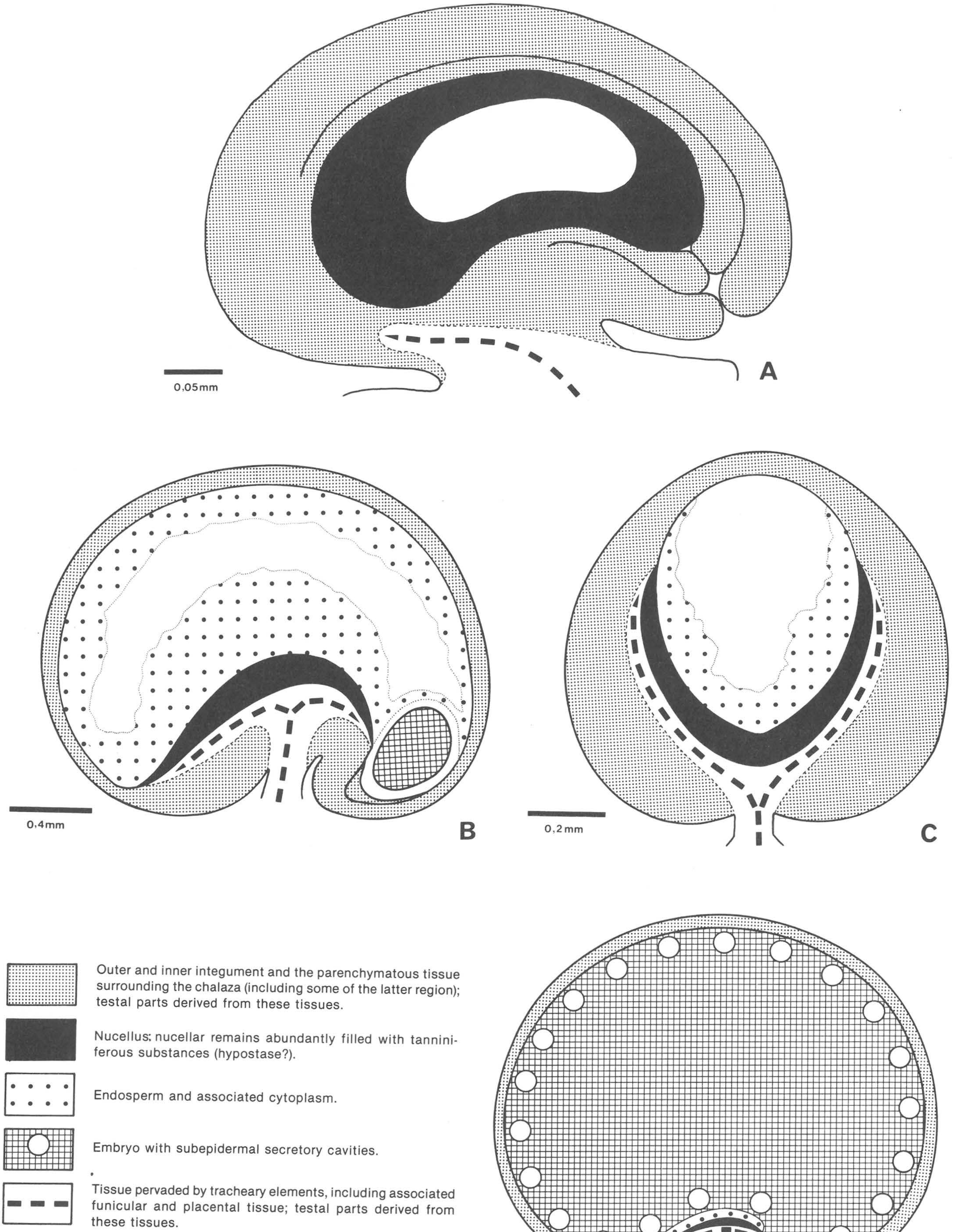


Figure 11A – D Ontogeny of seed type X. Successive stages of seed development in *E. simii* (*Van Wyk* 3296). A. Ovule, longitudinal section. B & C. Very young seed in longitudinal (B) and transverse (C) section — note remains of inner integument persisting in the micropylar region (compare Figures 13 & 15). D. Mature seed, longitudinal section.

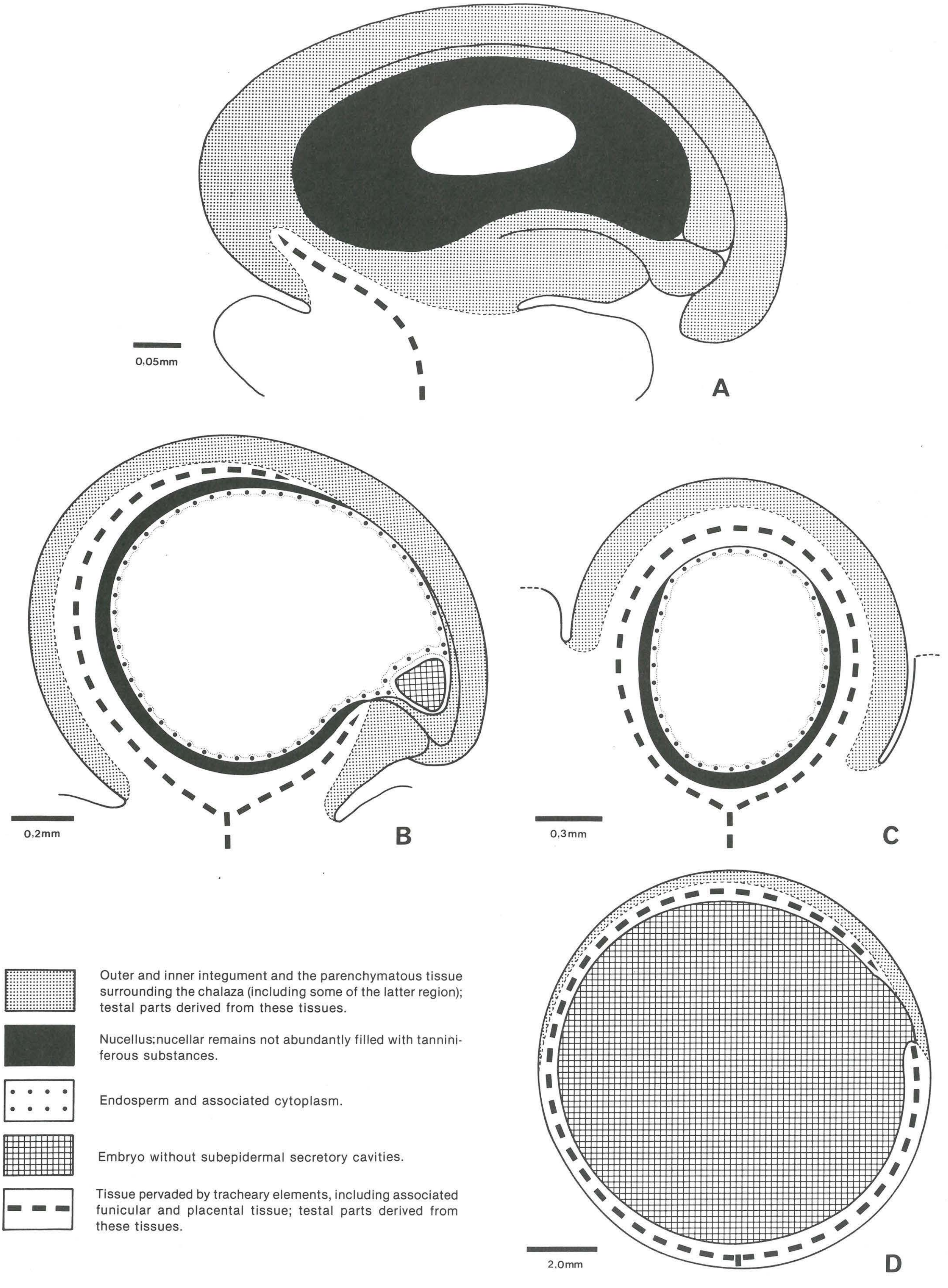
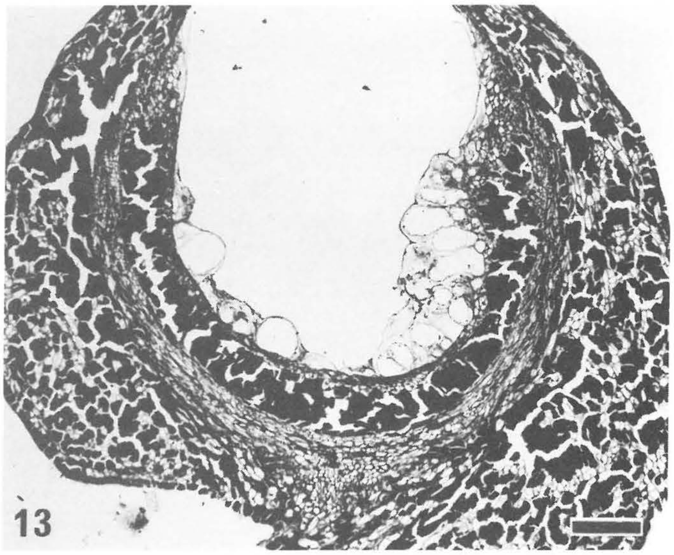
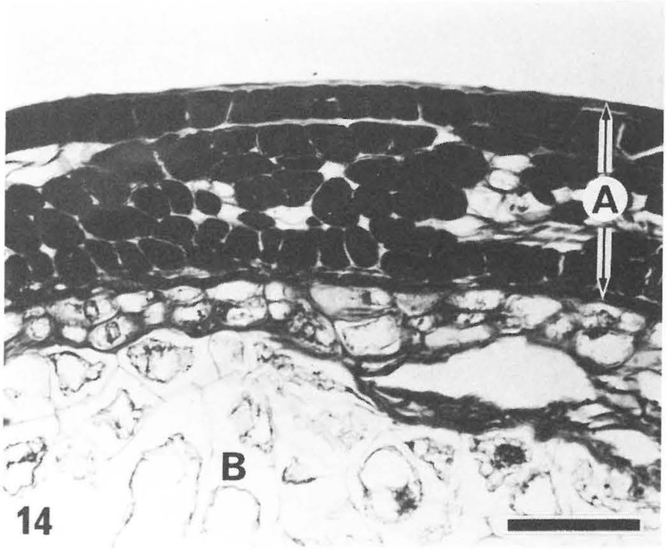
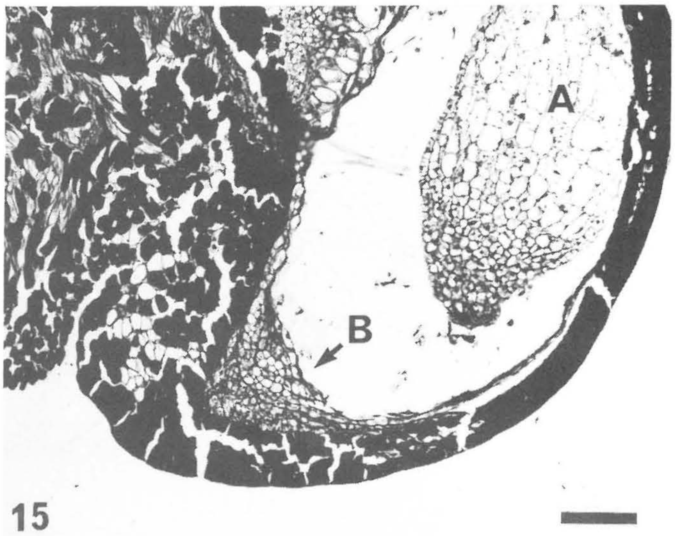
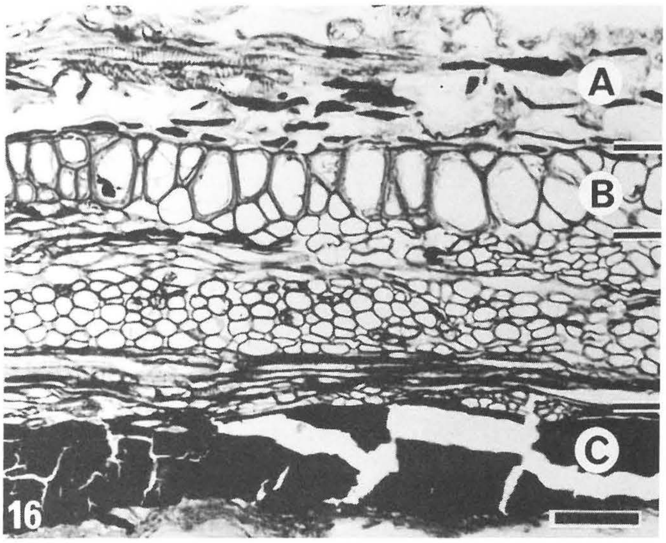


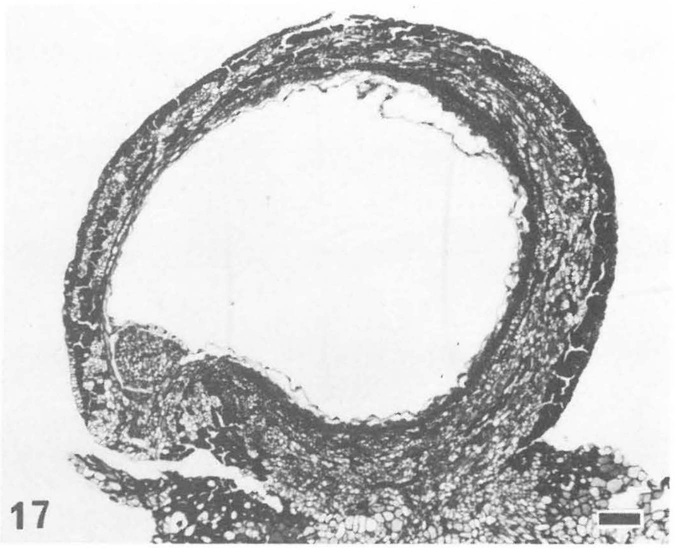
Figure 12A – D Ontogeny of seed type Y. Successive stages of seed development in *E. zeyheri* (*Van Wyk* 3134). A. Ovule, longitudinal section. B & C. Very young seed in longitudinal (B) and transverse (C) section — note remains of inner integument persisting in the micropylar region (compare Figure 17). D. Mature seed, longitudinal section — the lower half of seed represents the hilar hemisphere which was embedded in the placenta.

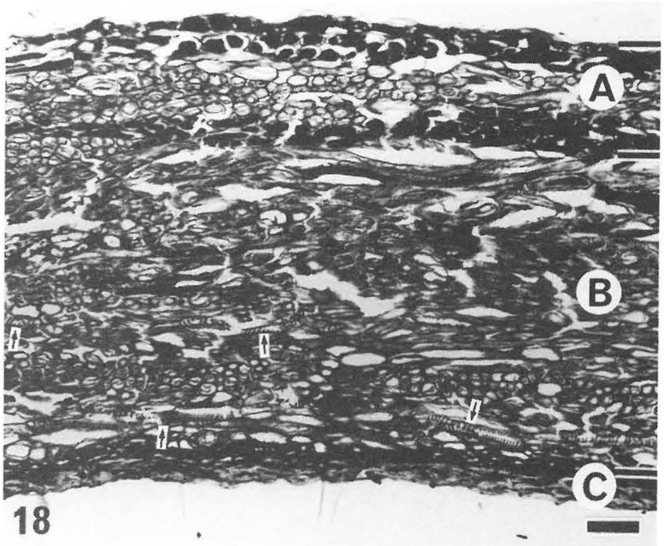




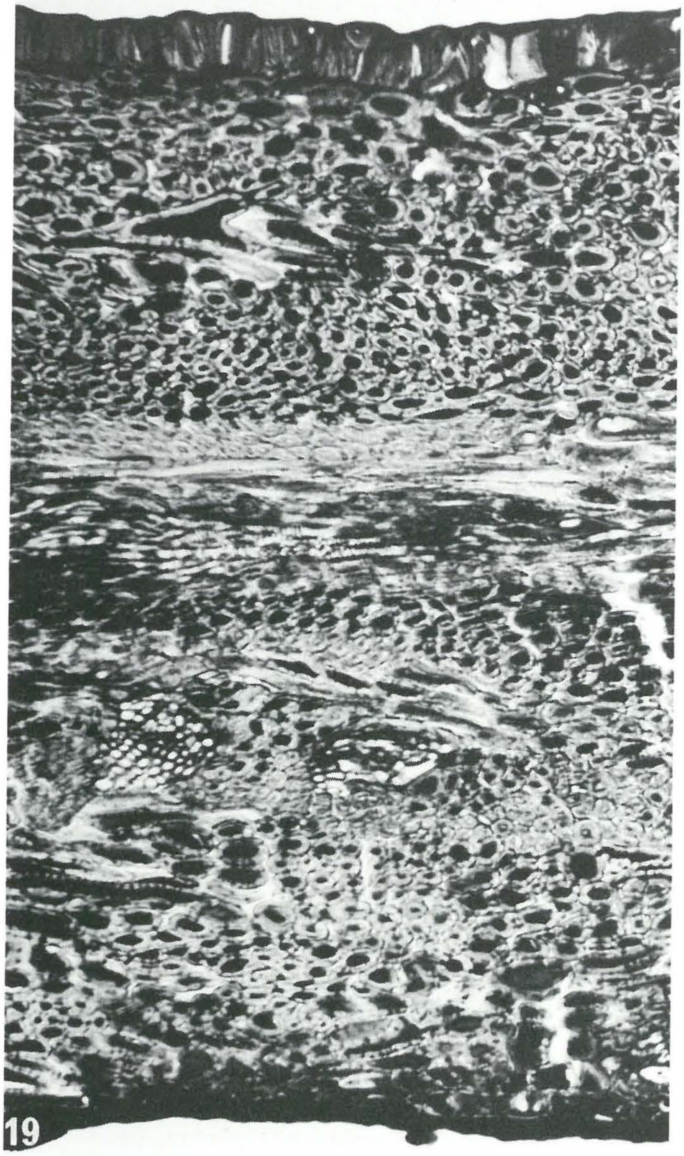








Figures 13 – 18 Morphology of the young seed. 13. *E. simii*, transverse section — compare with Figure 11C. 14. *E. simii*, longitudinal section showing the structure of the testa (A) and endosperm (B). 15. *E. simii*, longitudinal section showing the micropylar region — note embryo (A) and remains of the inner integument and probably nucellus (B) (all from *Van Wyk* 3296). 16. *E. capensis* (Van Wyk 2345), areolar region of testa in transverse section — note tanniniferous remains of the nucellus (hypostase?) (C), outer epidermal layer of developing macrosclereids (B) and adjacent pericarp with tracheary elements (A). 17. *E.* sp. C (*Van Wyk* 1303), longitudinal section — compare with Figure 12B. 18. *E.* sp. C (*Van Wyk* 3297), transverse section of testa — note subepidermal zone (A) of mesotesta (B), tracheary elements (some arrowed) and crushed remains of the inner integument and nucellus (C). Scale line = 100 μm (Figure 13, 15 & 17) or 50 μm (Figures 14, 16 & 18).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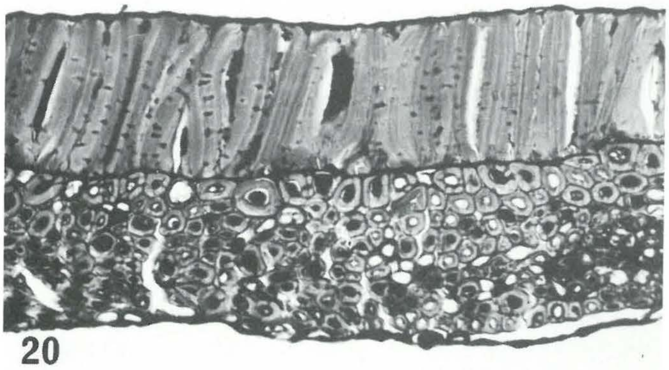
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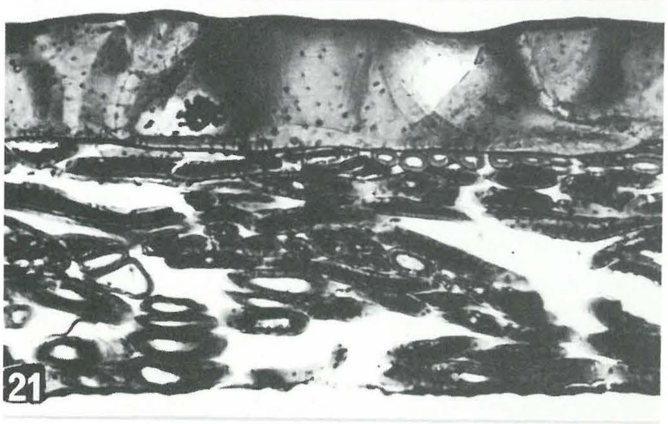
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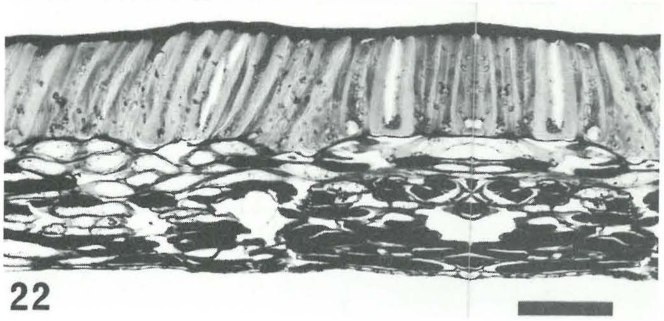
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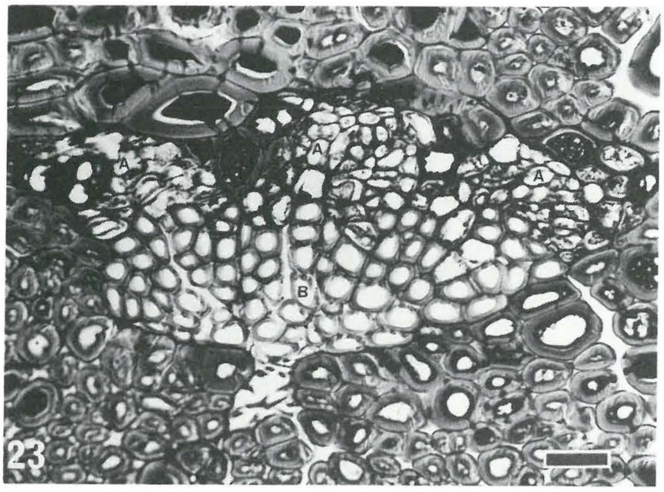

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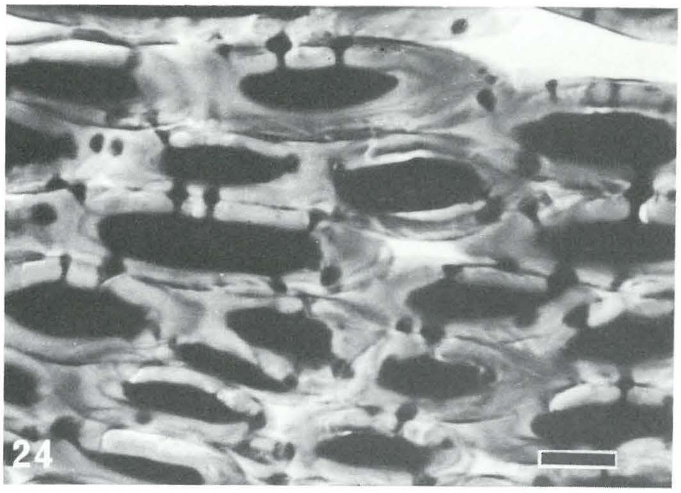
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Figures 19 – 24 Structure of the mature testa (transverse sections). Figures 19 – 22 on same scale to compare thickness. 19. *E. zeyheri* (*Van Wyk* 3134), note macrosclereids of outer epidermal layer (testa from micropylar hemisphere). 20. *E. simii* (*Van Wyk* 3296) showing epidermal macrosclereids and mesotesta of fibre-like sclereids with thick, lignified walls. 21. *E. umtamvunensis* (*Van Wyk* 3631) showing macrosclereids sectioned partly longitudinally — mesotesta as in Figure 20. 22. *E. natalitia* (*Van Wyk* 4854), mesotesta with most cells thin walled and unlignified (testa in last three figures from non-areolar region). 23 & 24. *E. albanensis*, testa of hilar hemisphere showing a vascular bundle with phloem (A) and xylem (B) in the former and sclereids of mesotesta with bordered pits in the latter (both from *Van Wyk* 5346). Scale line = 50 μm (Figures 19 – 22) or 20 μm (Figures 23 & 24).

fleshy cotyledons connected by a short radicular protuberance. The position of the areolae is reflected by matching impressions on the sides of the embryo.

The embryo is covered by a uniserial epidermal layer of relatively small cells overlayed by a thin cuticular membrane. All the free surfaces are abundantly dotted with secretory cavities (oil glands) (Figure 9B – E). These cavities occur just below the epidermis (Figure 11D) and first appear as clusters of tanniniferous cells. The formation of the cavities is at least initially schizogenous (Figures 27 – 30). The casing cells (Carr & Carr 1970) are usually strongly tanniniferous.

The remaining tissue of the embryo is parenchymatous and consists of more or less isodiametric cells. All these cells are abundantly filled with starch grains (usually hollow) in the mature embryo. In addition spherical bodies of unknown composition are also present in some specimens of *E. capensis* and *E. natalitia* (Figure 31). Histochemical tests for lipids and proteins were negative (Sudan black B and acid Fuchsin, respectively). In wax (stain: safranin O-fast green) and GMA (stain: PAS-toluidine blue) sections these bodies stain orange and greenish respectively. Druse crystals are rarely present.

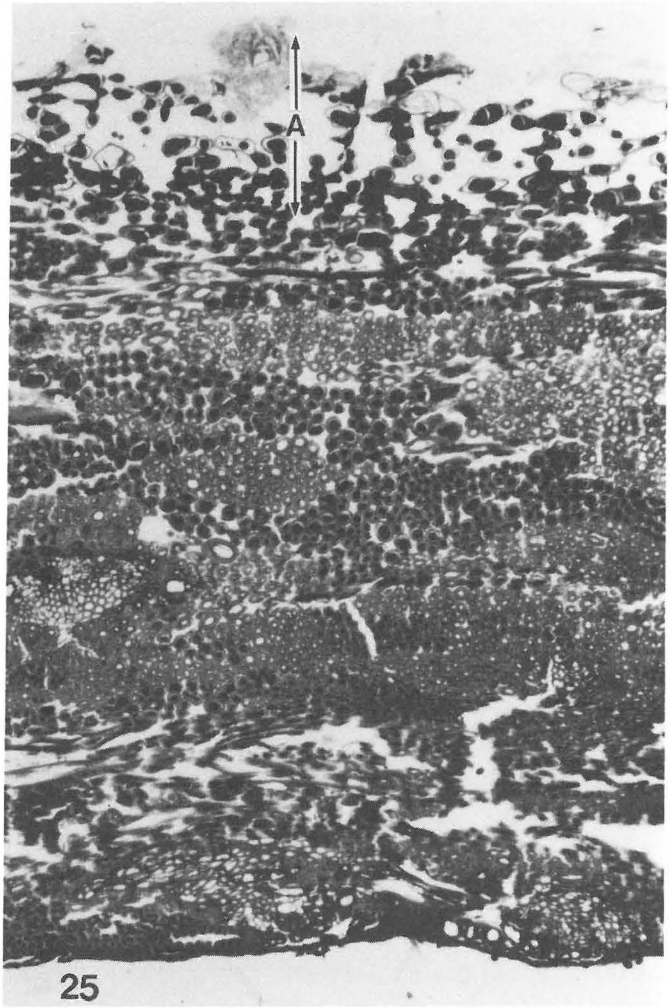
Endosperm formation is nuclear. The young seed cavity (before enlargement of the embryo) is almost completely filled with endosperm (Figures 11B & C, 13 & 14). Eventually the endosperm nuclei are apparently all separated by walls. Most of the endosperm is absorbed by the growing embryo, however, it is more persistent towards the periphery of the embryo sac in the areolar regions. Endosperm in the latter regions of the testa is usually clearly visible in mature seeds (Figure 11D).

3.3 Ontogeny of seed type Y

The first sign of seed development (Figure 12A – D) is a moderate enlargement of the ovule accompanied by a rapid extension of the hilar region. Owing to this expansion of the hilum and adjacent chalazal region (see below) the shape of the seed becomes globose (Figures 10A & 12D). The seed is sessile and the placenta becomes tanniniferous (if not already so) and highly vascularized. The mature seed is evidently overgrown with one hemisphere fused with the tissue of the laterally displaced placenta, septum and probably also adjacent pericarp. Considerable pressure is exerted by the growing seed and this obscures the boundary between septum and pericarp in ripe fruits. When the seed is removed from the fruit, one of the hemispheres is usually covered by the remains of this 'placental' tissue (Figure 10A). We call the latter region the hilum or hilar hemisphere of the seed and the remaining part the micropylar hemisphere.

The mature testa is rather thick and woody (cartilaginous?). It develops partly from the outer integument and the chalaza (Figure 12B & C). The inner integument is crushed although the micropylar part lasts slightly longer. During development the nucellus is gradually resorbed by the extended embryo sac and only a few crushed remains persist in the mature seed.

Numerous anticlinal and periclinal divisions of the mesophyll cells lead to an initial increase in the thickness of the integument. Similar divisions also occur in the outer epidermis. Periclinal divisions in the latter tissue tend to obscure the distinction between the epidermal and mesophyll cells.



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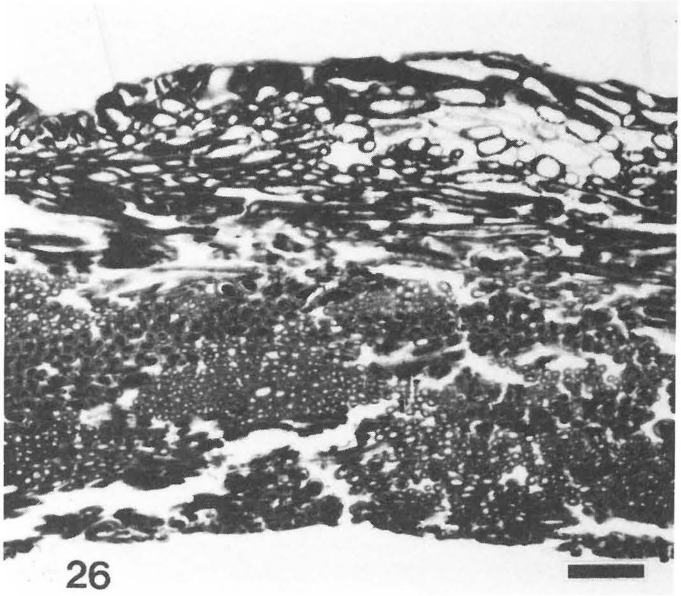

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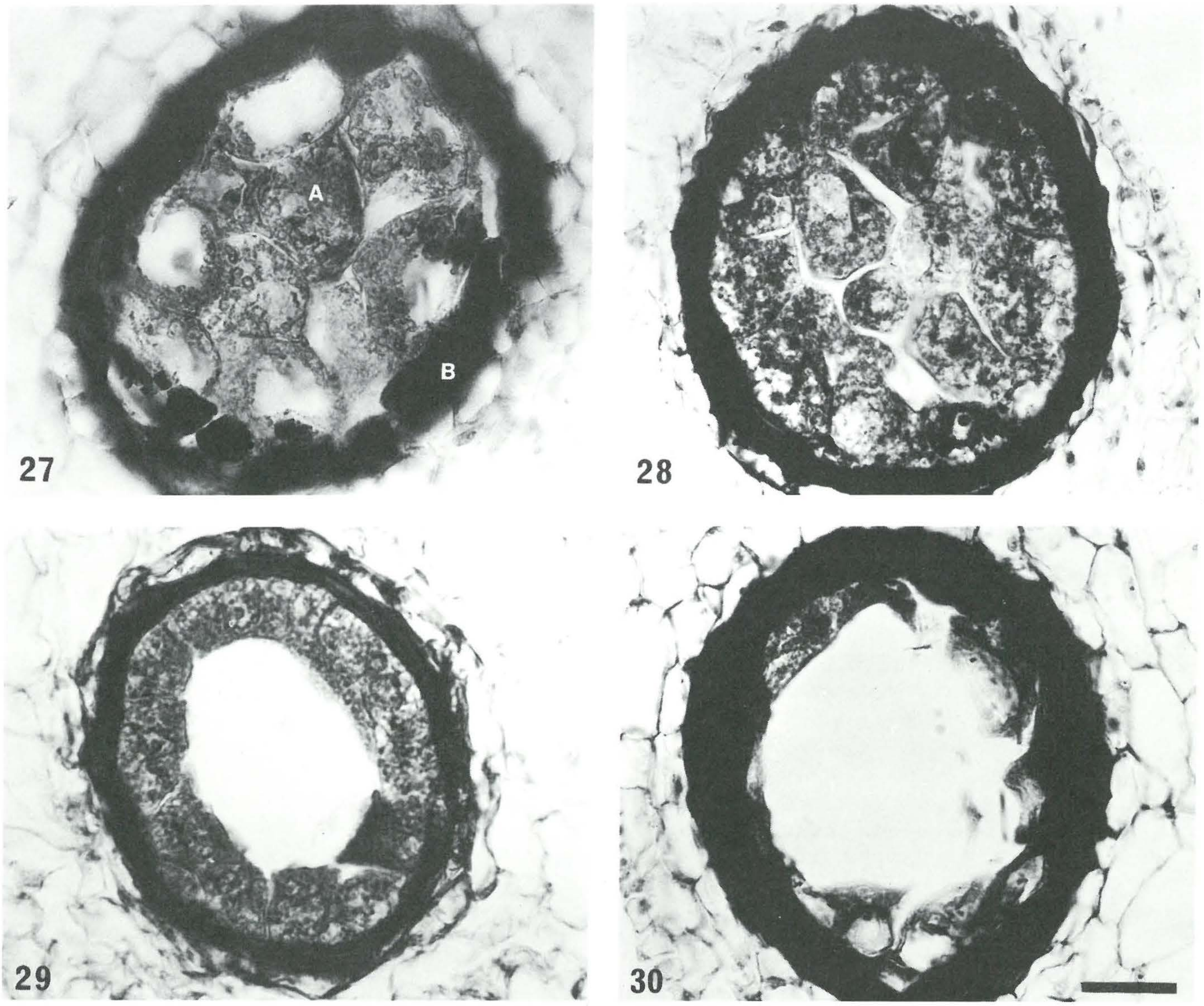
Figures 25 & 26 Structure of different parts of the mature testa in seed type Y. Transverse sections from same seed of *E. albanensis* (*Van Wyk* 5346). 25. Hilar hemisphere — note absence of subepidermal zone and parenchymatous remains of the placenta (A). 26. Micropylar hemisphere — note absence of a clearly differentiated layer of epidermal macrosclereids in this specimen (compare with Figure 19). Scale line = 100 μm.

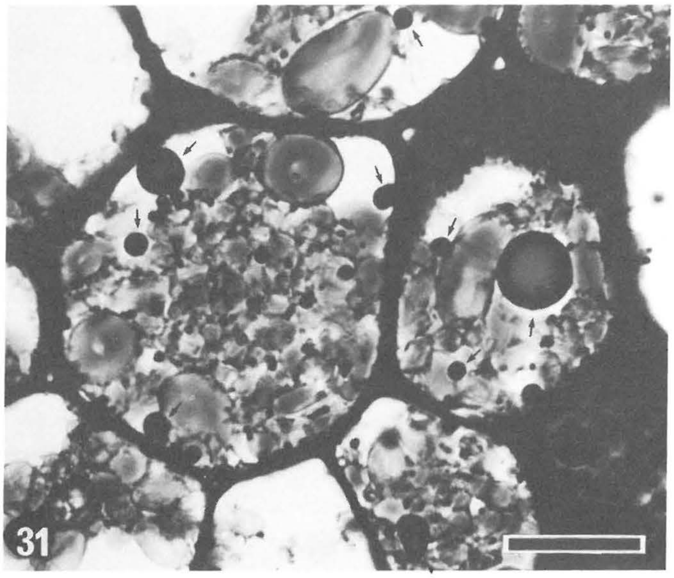


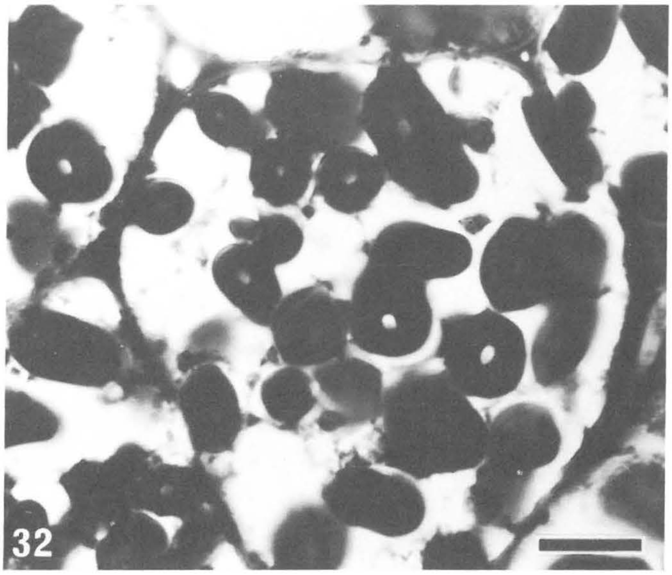
Figures 27 – 30 Stages in the development of secretory cavities in embryo of seed type X. Transverse sections of cotyledons of *E. capensis* (*Van Wyk* 2343). 27. Young secretory cavity with central epithelial cells (A) surrounded by casing cells (B). 28. Interior walls between epithelial cells separating to form cavity. 29. Older secretory cavity with epithelial cells lining the central cavity. 30. Secretory cavity with epithelial cells showing signs of damage (lysis?). Scale line = 20 μm.

However, the divisions are predominantly anticlinal in some specimens. A subepidermal mesophyll zone of larger cells (some derived from periclinal divisions from epidermal cells) can be distinguished (Figures 12B – D & 18). Clusters of tanniniferous and non-tanniniferous cells (each apparently derived from different parent cells) are usually present in this zone and are eventually responsible for the mottled appearance of the testa (micropylar hemisphere) in some seeds.

As the above-mentioned thickening of the integument proceeds, there is a considerable increase in cell division and elongation in the chalazal region (Figures 12B & 17). This expansion of the chalaza coincides with, and is probably responsible for, the expansion of the hilum. Vascular bundles derived from the extensive vascular supply of the placental region enter the chalaza where they spread out and form an intricate vascular network (Figure 23). Extension of this vascular tissue gradually proceeds towards the micropyle (Figure 12B). This extension is preceded by a wave of intercalary growth within the inner layers of the mesophyll, proceeding from the expanded chalaza, and resulting in a considerable increase in the thickness of the developing testa. The greater part of the testal mesophyll is formed by this intercalary growth (Figure 18). It remains to be confirmed whether the latter vascular and associated tissues develop from the mesophyll of the outer integument (which we assumed) or whether it is chalazal tissue which penetrates the mesophyll by means of intrusive growth. See also 4.3 for a possible alternative interpretation. At this stage the testa of the developing seed consists of two parts, *viz.* a hemisphere derived from the chalaza (the hilar hemisphere) and a hemisphere derived from the outer integument and probably also chalaza (the micropylar hemisphere). With the exception of a small area in the micropylar region, both halves are pervaded by vascular tissue. Seed type Y may therefore be described as at least partly pachychalazal (Figure 12D).

A clearly defined outer epidermal layer has not been observed in the hilar hemisphere of the mature seed (Figure 25). However, in the micropylar hemisphere the degree to which the epidermal layer is demarcated from the mesotesta is rather variable. A well differentiated epidermal layer of radially elongated fibrous cells (as in seed type X) has been noted in *E. zeyheri* and *E. zuluensis* (Figure 19). The radial and inner





Figures 31 & 32 Structure of mature embryo (transverse sections of cotyledons). 31. *E. natalitia* (*Van Wyk* 4554) showing starch granules and unidentified spherical bodies (some of the latter arrowed); embedded in GMA and stained with PAS-TP. 32. *E. zeyheri* (*Van Wyk* 2180) showing only starch grains — note hollow centres; embedded in GMA and stained with IKI. Scale line = 10 μm.

tangential walls of the epidermal cells are thick, lignified and richly pitted (bordered pits). Outer tangential walls are occasionally affected. The presence of a differentiated epidermal layer is apparently linked to the frequency of periclinal divisions in the developing epidermal cells. If the frequency is high, the fibrous sclereids of the outer layer barely differ from, or are similar to, those of the adjacent mesophyll (Figure 26).

The mesophyll cells of the young testa develop similarly to those of seed type X, into fibrous sclereids with thick lignified walls containing numerous bordered pits (Figure 24). These sclereids (fibre tracheids?) are often tanniniferous. However, many more sclereids are formed resulting in a thick, multilayered woody testa (Figures 19, 25 & 26). The integument of seed type Y may therefore be described as multiplicative. The seed is also mesotestal because the mesophyll constitutes the main mechanical layer.

In sections the testal tissue of the hilar hemisphere is similar to the bulk of tissue in the micropylar hemisphere. However the fibrous sclereids which develop from the subepidermal zone in the latter hemisphere occasionally tend to be thicker and differently stained (Figures 25 & 26).

The thickness of the testa often decreases slightly from the hilum towards the micropyle. A short, shallow depression extending dorsally from the micropyle is clearly visible from the inside of the testa (Figure 10E). In this area the testa is more lightly coloured, often mottled, relatively thin and traversed by few or no vascular elements (Figure 12D). Pressure exerted by the expanding embryo against the inner surface of the testa is probably partly responsible for retarding the thickening of the testa in this region. We could also find little or no indication in this region of the intercalary growth which occurs in the mesophyll of the rest of the testa (an alternative interpretation of the origin of the depression is discussed under 4.3). The micropyle is always situated on the border between the two hemispheres (Figure 10A). In the mature seed it is nearly always closed, rarely an open pore, and therefore rather difficult to detect from the outside. However, the position of the more lightly coloured and often mottled patch of testa forming the depression can be used as a guide.

The morphology of the mature embryo (Figure 10B – D) is described by Van Wyk (1980). Its initial slow increase in size, location next to the micropyle (Figure 12B) and eventual rapid expansion resemble the situation in seed type X. The most significant difference between the two types of embryo is probably the secretory cavities which are nearly always lacking in the embryo of seed type Y (Figure 12D). A few secretory cavities restricted to the radicular protuberance have only been observed in a few embryos, notably those of *E. zeyheri*. The position of the micropylar depression of the seed coat is matched by a raised area of tissue in the vicinity of the radicular protuberance (Figure 10B). With the exception of the epidermal cells, starch grains (usually hollow) are abundantly present in the parenchyma cells of the embryo (Figure 32). Spherical bodies similar to those in seed type X (see 3.2) have not been observed.

Endosperm formation is of the nuclear type. The nuclei are sparsely distributed in a thin layer of cytoplasm along the periphery of the embryo sac (Figure 12B & C). Wall formation has been observed in the micropylar region but it could not be established whether the endosperm eventually becomes cellular throughout. Nevertheless, it is clear that the amount of endosperm formed is considerably less than in seed type X. Endosperm can no longer be seen in the mature seed (Figure 12D).

3.4 Structure of the ovulodes

Although one seed usually develops in an ovary, the abortive ovules persist as ovulodes and can therefore be detected in ripe fruits of both species group X and Y. The ovulodes are crowded against the wall of the pericarp by the developing seed and are often difficult to find in the relatively fleshy fruits of species group Y. Most of the flattened ovulodes are more or less the same size as the original ovules. However, larger ovulodes are occasionally present. It often seems as if more than one ovule starts to develop but one gains dominance and the development of the others is suppressed. Despite being considerably compressed, the structure of the ovulodes is rather similar to that of the ovule (Figure 6). There is a variable increase in the number of cells of the outer integument and nucellus. Cell walls thicken slightly but we could find no evidence of lignification. Most of the cells are abundantly filled with tanniniferous substances. This explains the brownish colour of the ovulodes in fixed material.

4. Discussion

4.1 General

Morphological characters of the mature embryo were first employed by De Candolle (1828) in his subdivision of the tribe Myrteae into three principal groups. These groups were subsequently treated as the subtribes Myrcioideae, Eugenioideae and Pimentinae (Berg 1855/56, 1857 – 59). According to the International Code of Botanical Numenclature the correct names for these subtribes are Myrciinae, Eugeniinae and Myrtinae (McVaugh 1968). These names were used among others by Niedenzu (1893) in the last monograph of the Myrtaceae. Based upon the three types of embryo structure originally recognized, it has become common practice to refer to the myrcioid, eugenioid and pimentoid (myrtoid) type of embryos.

A new classification of the Myrtaceae was proposed by Kausel (1956). He distinguished between the succulent fruited Myrtaceae (tribe Myrteae) and capsular fruited Leptospermaceae. Kausal divides his Myrtaceae into five groups which were later designated as subfamilies (Kausal 1967). A sixth subfamily was later segregated from the Eugenioideae (Kausel 1957a). The classification and delimitation of new genera proposed by Kausel are almost exclusively based on the mode of seed germination and embryo structure. Many of Kausel's subfamilies are recognized by Melchior (1964) but at tribal level.

Briggs & Johnson (1979) provide a comprehensive treatment of inflorescence structure in the Myrtaceae. They present the results of their survey within a suprageneric framework consisting of informal alliances. Within their Myrtoideae the alliances and suballiances largely agree with Kausel's arrangement. However, they stressed the need for further comparative study of the embryo, fruit and other characters.

Warning against too much emphasis on mainly embryonic characters and the resultant danger of creating artificial groups has already been voiced by Bentham (1869). In this regard Kausel's classification was particularly criticized by McVaugh (1968) among others. McVaugh proposed a new subdivision of the American Myrteae based mainly on a combination of embryo, seed coat, flower and inflorescence characters. The traditional subtribes were abandoned and the genera arranged in six groups without formal taxonomic rank. A number was assigned to each group. In addition eight genera which apparently represent distinct lines of descent from the same protomyrtaceous stock were recognized. Genera of group 1 are characterized by the myrcioid group 2 and 3 by the eugenioid and group 4, 5 and 6 by the pimentoid type of embryo.

The majority of genera and species of the Myrteae are restricted to the New World. The genus *Eugenia s. str.* has several hundred species in tropical America and relatively few in Africa and the rest of the Old World. It is one of the most difficult genera to define and a satisfactory delimitation of the genus on a world-wide basis has not yet been accomplished. Views on the taxonomic treatment of taxa in the New World should therefore be considered before judgement can be passed on taxonomic problems among taxa from the Old World.

Judging from the general taxonomic accounts of *Eugenia* in other parts of the World, it is evident that the fruit and seed are known only in relatively few species. Descriptions of the fruit and seed are usually vague and refer only to gross morphological features. Notable exceptions include the regional revisions of Henderson (1949) and Wilson (1957). Today, however, the majority of species described by them are referred to *Syzygium* Gaertn. and other segregate genera. Species of *Eugenia* in America have also repeatedly been transferred to various taxa of different ranks. All these make a meaningful comparison between *Eugenia* in Africa and the rest of the world difficult if not impossible at this stage. We have nevertheless attempted to compare our data with the rather limited literature available to us. In this connection we have relied heavily upon the excellent report of McVaugh (1968). The embryo of seed types X and Y is without doubt of the eugenioid type (see also Van Wyk 1980 for a detailed description of the mature embryo). The generic identity of the investigated species must therefore be sought mainly within group 2 and 3 of McVaugh, the Eugenioideae, Plinioideae and Acmenoideae of Kausel or the *Eugenia* and *Acmena* alliance of Briggs & Johnson.

Despite the considerable taxonomic value attributed to characters of the seed in the Myrteae, little attention has been directed to seed histology and development. The thesis of Petit (1908) is one of the pioneer studies in this field. Unfortunately most of the species studied belong to the Leptospermoideae. Only one of his species, *Stenocalyx michelii* Berg is currently treated as a species of *Eugenia viz. E. uniflora* L.

Most of the early references to ovule structure and development in *Eugenia* are mainly concerned with the phenomenon of polyembryony (for references see Netolitsky 1926, Davis 1966, Corner 1976). However, these *Eugenia* species are currently probably all referred to *Syzygium*. Recent ontogenetic studies of myrtaceous seed include those of Hartley & Craven (1977) on *Acmena* DC. and Landrum (1982) on *Campomanesia* Ruiz & Pavón.

4.2 Ovule structure, placentation and miscellaneous features

A bilocular ovary, as in the southern African species of *Eugenia*, is most common in many of the Myrteae. According to our observations, unilocular and trilocular ovaries are rare, often restricted to a particular plant and probably best regarded as anomalous. A compitum is very common in Myrtaceae and occurs in most genera (Carr & Carr 1961; Schmid 1972a & b; Wilson & Waterhouse 1982). Placentation agrees with the descriptions for *Eugenia* from the New World (e.g. McVaugh 1963b). According to Schmid (1972a, b & c) species of *Eugenia s. str.* have a transeptal vascular supply to the ovules whereas that of *Syzygium s.l.* is axile. The present study as well as additional observations on southern African species of *Syzygium* (unpublished data) support these findings.

Ovular structure, presence of ovulodes and mode of endosperm formation in species groups X and Y conform in general to the conditions described for Myrtaceae (Netolitsky 1926; Mauritzon 1939; Davis 1966; Corner 1976; Schmid 1972a & 1980). The observed accumulation of relatively large druse crystals within ovules is probably an anomalous condition. Those *Eugenia* species for which only a single integument has been described in the literature, can probably all be referred to *Syzygium*. The lack of air gaps between the two integuments and between the inner integument and nucellus could be an artifact caused by fixation (Corner 1976, p.19).

The number of ovules per locule appears to be taxonomically significant in the Myrteae — but to what extent is not yet fully known (McVaugh 1968). For example, genera of McVaugh's group 1 are nearly always biovulate while those of group 2 and 3 are nearly always multiovulate. In *Eugenia* (group 2) there are usually many ovules per locule and rarely as few as one to three in each locule; e.g. in *E. chinajensis* Standl. & Steyerm., *E. coffeifolia* DC., *E. conjuncta* Amsh. and *E. dentata* (Berg) Niedenzu (McVaugh 1963a & b, 1968, 1969). However, within McVaugh's group 2 and 3 the reduction of the number of ovules to two is characteristic for species of *Myrciaria* Berg and *Plinia* L.

In agreement with their New World counterparts, *Eugenia* in the Old World (excluding Africa), and in particular those species previously referred to *Jossinia* DC., usually appears to be multiovulate, i.e. 10 – 20 or more ovules per locule (Blume 1849 – 51; De la Bâthie 1953; Scott 1980). However, exceptions do occur, e.g. *E. anjouanensis* H. Perr. from the Comores is described as biovulate (De la Bâthie 1953).

Ovule number has rarely been mentioned in descriptions of African species of *Eugenia* (e.g. Engler 1899; Dümmer 1912; Engler & Von Brehmer 1917). Many generic descriptions nevertheless refer to the locules as multiovulate (e.g. Lawson 1871; Sonder 1894; White 1978). However, we regard generic descriptions as an unreliable source of information because it seems as if many authors have uncritically copied existing descriptions from other parts of the world.

Amshoff (1974) described *E. ancorifera* from Cameroun as 'pauciovulatum'. The illustration shows two sessile ovules per locule. This agrees with the situation in the southern African species of *Eugenia*. It nevertheless seems as if the number of ovules tends to be low (2 – 6) in African species of *Eugenia*. This was confirmed by a rather limited preliminary investigation of specimens to the north of our area (unpublished data). Almost all the latter specimens belong to species group X.

Variation in ovule number from two to many has been reported in other large genera of the Myrteae, e.g. *Myrceugenia* Berg (Landrum 1981). Therefore low ovule number as such is probably not taxonomically very significant. However, its constant occurrence (especially in species group Y), correlation with a number of other characters and apparent geographical restriction considerably increase the taxonomic value of this character state in African material.

Little is known about the variation in ovule type among the genera of the Myrteae. Corner (1976) described the ovules of *Eugenia s.l.* as anatropic. However, most if not all of the species listed by him under that genus are currently treated as species of *Syzygium*. Existing descriptions should also be treated with caution because we believe that campylotropous ovules have frequently been taken as anatropous during cursory investigations. The only southern African species of *Eugenia* previously studied embryologically appears to be *E. capensis* (Mauritzon 1939). Unfortunately the species is merely mentioned without any detailed account of its ovule morphology.

We have found the ovule terminology proposed by Bocquet & Bersier (1960) (see also Bocquet 1959) very useful to classify the ovular type in the native species of *Eugenia*. Guédés (1979), among others, regrets the fact that this system has not yet been adopted more widely. Although the proposed terminology has for example been taken up by Davis & Heywood (1963), it has unfortunately not been widely used by subsequent workers. Bocquet & Bersier stress the mode of ovule development. However, we based our conclusions indirectly on the course of the vascular strand in the mature ovule (see also Foster & Gifford 1974).

According to Bocquet (1959) the campylotropous ovule can be rendered amphitropous by the local proliferation of tissue (raphe and integument) on the ventral side of the seed. This hump of tissue has been called the basal body and it is allegedly partly responsible for raising the floor of the nucellus. We can, however, not agree with the view of Foster and Gifford (1974) that the basal body is synonymous with the hypostase.

The ventral pad of tissue in seed type X borders the hilum and is pervaded by vascular strands spreading out from the funicle. We consider this tissue as homologous with the so-called basal body. There is probably a need for a more appropriate term for this pad of tissue because it eventually expands laterally to the sides of the seed where it forms the areolae. A hypostase in the sense of Dahlgren (1940) and Maheswari (1950) is not present in the investigated species.

The extensively developed chalazal tissue in seed type Y could be homologous with the basal body which has almost completely pervaded the seed coat. It could also be that the branching mass of intercotyledonary 'placental (or funicular)' tissue in *Acmena* (Hartley & Craven 1977), *Piliocalyx* Brongn. and *Acmenosperma* Kausel (Kausel 1957a) is an extension of a similar tissue.

4.3 Structure of the testa

According to McVaugh (1968) the testa in *Eugenia* is very thin, membranous or leathery. This also applies in general to the other genera referred to the Eugeniinae by Berg. Merril & Perry (1939) described the texture of the testa in *Eugenia* as being 'smooth, chartaceus to cartilaginous'. Although we have described the relatively thin testa of seed type X as being leathery, opinion could differ on this point. Owing to the lignification of the cells the testa can be rather brittle, especially when dried out. However, to describe the testa as membranous (Van Wyk 1980) is to exaggerate.

Petit (1908) described the seed coat of *E. uniflora* (= *Stenocalyx michelii* Berg) as completely parenchymatous. Our own observations of this species (unpublished data — voucher specimen: *Van Wyk* 1310 in PRU) show that the cells of the mature testa are all lignified and not parenchymatous at all. We must stress the fact that lignification of the testal tissue occurs only at a comparatively advanced stage of seed development. Comparative studies based on seeds from herbarium specimens should be done with great caution. Seeds can be quite large and apparently mature (because of its overgrown nature) when in fact lignification has not yet started or is still incomplete. In our experience ripe fruits with mature seeds are generally rare in herbaria. In nature ripe fruits are rapidly removed from trees by birds, monkeys, baboons etc. and are therefore difficult to collect. In addition ripe fruits are frequently lost during the preparation of herbarium specimens.

The testa of *E. salamensis* Donn. is described as thick-cartilaginous (McVaugh 1963b). However, a thick woody testa as encountered in seed type Y does not seem to be a characteristic feature of *Eugenia* and related New World genera. As far as could be ascertained, a pachychalazal seed coat has apparently not previously been recognized in the Myrtaceae. In this respect species group Y could be unique among the Myrteae. Corner (1976) nevertheless speculates that the seed coat in unitegmic species of *Eugenia* (probably *Syzygium* in our present conception) may be pachychalazal. However, very little is known about the histology of the seed coat in the Myrteae and a pachychalaza may still be discovered in other genera. Furthermore, no previous reference to an extended hilum (hilar seed) in the Myrtaceae could be traced. Kausel (1956, p.504) described the testa of his new genus *Pseudomyrcianthes* as 'testa chartacea partim pericarpo adhaerens'. Whether this adherence to the pericarp signifies an extended hilum is unknown and doubtful. The latter genus is incidentally in part referred to the synonymy of *Eugenia* section *Pilothecium* (Kiaersk.) Legrand by Legrand (1975).

In seed type Y the origin of the thin, whitish or mottled area of testa lining the depression in the vicinity of the micropyle needs further investigation. It is possible that this patch of testa is the remaining free part of the integument(s) which has expanded but little during the growth of the seed. This would mean that all of the remaining part of the testa has developed from the chalaza by intercalary growth. The subepidermal zone of mesophyll tissue (see 3.3) would then represent the tissue which normally surrounds the chalaza. In the words of Corner (1983): ' . . . the chalaza is the internal region of the seed (or ovule) which unites the integuments and nucellus; it has no outside'.

According to Van Wyk (1980), the testa in seed type Y is thinner in the hilar hemisphere than in the micropylar hemisphere. This statement is based on an erroneous observation as the thickness of the testa often decreases gradually, although slightly, towards the micropyle. However, if the seed is viewed from the outside, the surface of the hilar hemisphere is often slightly lower with respect to the rest of the testal surface. This is probably due to the lack of a clearly defined epidermal layer in the former region.

In southern African species of *Eugenia,* Van Wyk (1980) regards the testa as being free from the pericarp in ripe fruits. Obviously this statement only partly applies to seed type Y. In the present study it was also found that the testa in immature and even mature fruits of *E. capensis* (seed type X) usually tends to adhere to the pericarp. This adherence is partly brought about by the pressure of the seed against the inner layers of the pericarp and is particularly evident before lignification of the testa has been completed. The possibility that the developing seed derives some nourishment from the adjacent pericarp directly through the immature testa needs investigation. In this connection tracheary elements in the pericarp have frequently been noticed quite close to the epidermal layer of especially the vascularized areolar surface of the testa (Figure 16). The degree of adherence between pericarp and testa apparently also depends on the extent to which the epidermal layer of the testa is differentiated. If the epidermis consists of a well defined layer of macrosclereids the pericarp can usually be completely removed from the testa. If not, the testa and pericarp tend to adhere, especially in the immature seed.

4.4 Structure of the embryo

The embryo of both seed type X and Y consists of two fleshy, partly fused cotyledons connected by a short radicular protuberance and can therefore be classified as the eugenioid type. In *Eugenia* and related genera the degree of fusion between the cotyledons needs to be studied critically. Available references on this aspect are usually vague and rather unsatisfactory for comparative purposes. The cotyledons, for instance, have been described as united (Merril & Perry 1939); usually fused i.e. pseudomonocotyedonous (Schmid 1972a); and apparently homogeneous but often showing the line of separation between the two planoconvex cotyledons (McVaugh 1968). According to Briggs & Johnson (1979) some Old World species formerly included in *Jossinia* have separate cotyledons (e.g. *E. oraria* Guill., *E. indica* Wight), whereas in others the cotyledons are completely or partially fused.

We have examined mature seeds of the American *E. uniflora* (see 4.3). The cotyledons in this species are partly fused with a short external line of separation thereby resembling the embryos in southern African species of *Eugenia*. However, Kausel (1956) in his key to the genera of the Eugenioideae characterized the embryo of *Eugenia s. str.* as 'ungliederter Embryo' (ungegliederter?) and that of *Pseudomyrcianthes* and *Myrciaria* as 'Embryo mit kleinem interembryonalem Spalt'. Furthermore *Pseudanamomis* Kausel is described as having 'cotyledones magnae, subinaequales, latere ventrali ad radiculam versus parte circiter 1/3 connatae, caeterum liberae'. The latter genus is, however, placed by Kausel under his Plinioideae which is characterized by large fleshy cotyledons which are separate! Legrand (1975) discusses this intolerant interpretation and mentions that he knows of several South American species of *Eugenia* and *Myrciaria* of which the cotyledons show variable degrees of fusion — even within the same species. Legrand comes to the conclusion that the partial fusion (or separation) of cotyledons has no taxonomic value at all — at least not in that region. *Pseudomyrcianthes* is subsequently reduced by Legrand (at least in part and including the type species) to *Eugenia* section *Pilothecium* (Kiaersk.) Legrand.

Following the examination of a very large number of seeds from southern African species of *Eugenia*, no seed with either completely free or completely fused cotyledons has been found. They are always partly fused (Van Wyk 1980). A cursory study of rather limited material of *Eugenia* from tropical Africa (unpublished data) indicates a similar condition although the external line of separation is apparently absent in some embryos. Amshoff (1958) regards the split at one side of the embryo in *E. klaineana* (Pierre) Engl. and *E. gabonensis* Amsh., an unusual character among the *Eugenia* species of French Equatorial Africa. Certainly in southern African species of *Eugenia* the reverse applies.

Marloth (1925) provided an illustration of *E. natalitia* (Plate 75) which depicts free cotyledons covering a plumule and radicle. *E. natalitia* is undoubtedly a misidentification. Both the illustrated branchlet with ripe fruits and the seed are rather those of an exotic species of *Syzygium*.

Another neglected character of the embryo in the Myrteae is the occurrence of secretory cavities. It is not even mentioned by Kausel (1956) who relies so heavily on the morphology of the embryo for the delimitation of genera. What appears to be a few secretory cavities has been noticed only in his drawing of the embryo in *Myrcariopsis baporeti* (Legrand) Kausel. In his anatomical study of the fruit and seed in the Myrtaceae, Petit (1908) concluded that the embryo of *E. uniflora* (= *Stenocalyx michelii* Berg) is without secretory cavities. However, this is contradicted by our own observations of this species (naturalized in our area). We have found that the embryo has all free surfaces abundantly dotted with secretory cavities. In this respect it resembles seed type X. Judging from Petit's Figure 45 we are almost sure that the same species is involved since the sulcate fruit is an outstanding feature for this species. This apparent discrepancy needs further investigation. As far as seed type X is concerned, secretory cavities are always abundantly present in all the investigated embryos — even in slightly immature ones.

Van Wyk (1980) described the embryo of seed type Y as apparently eglandular. The present study has confirmed the lack of secretory cavities in the cotyledons. A few secretory cavities have been observed so rarely in the vicinity of the radiccular protuberance (especially in *E. zeyheri*) that their presence can be regarded as anomalous. The eglandular nature of the embryo is still evident a few weeks after the seed has germinated (unpublished data).

Whether the secretory cavities in the Myrtaceae arise schizogenously, lysigenously or schizo-lysigenously has long been a matter of controversy (for references see Carr & Carr 1970). Recent studies (Carr & Carr 1970; Brocheriou & Belin-Depoux 1974) show clearly that the formation is schizogenous.

Carr & Carr (1970) reported that the formation of the intercellular oil cavities in the glands of eucalypt embryos is first noticeable a few days after the beginning of germination. In *Eugenia*, however, these cavities are fully developed in the mature embryo and usually filled with oil. A little granular tanniniferous substance has occasionally been observed. The latter has most probably been derived from damaged epithelial cells lining the cavity. The delicate walls of these cells were often torn in both wax and GMA embedded material. This 'lysis' of the cells could be ascribed to poor fixation with FAA, but needs further investigation. The initial formation of the secretory cavities is, however, without doubt schizogenous.

Little is known about the kind of reserve foods stored within the embryos of the Myrteae. In the investigated material of *Eugenia* starch in the form of hollow grains is the principal storage product. These resemble the ones described from the wood of the southern African species of *Eugenia* (Van Wyk *et al.* 1983). The composition of the spherical bodies in some embryos of *E. natalitia* and *E. capensis* could not be determined. The possible taxonomic sigificance of these bodies remains undecided and needs further study.

As in other parts of the Old World, seeds of *Syzygium* in southern Africa are often polyembryonic. This was already noted by Henderson (1949) in our most common species, *S. cordatum* Hochst. However, we have found no evidence of polyembryony in the southern African species of *Eugenia*.

4.5 Endosperm

The observed nuclear endosperm corresponds with the accepted condition in the Myrtaceae (Mauritzon 1939; Davis 1966). According to Corner (1976) the mature seeds of the Myrtaceae are almost or quite exalbuminous. The subtribe Orthostemonoideae was introduced by Berg (1855/56) to accommodate those American species of the Myrteae with endosperm in the seed. Two species of *Feijoa* Berg { = *Orthostemon* Berg (1856) non *Orthostemon* R. Br. (1810)} were referred to this group.

The work of Petit (1908) has shown that traces of endosperm are present in many myrtaceous seeds. In his opinion the amount of endosperm in seeds of *Feijoa* is not significantly more or less than in genera such as *Myrtus* L. and *Psidium* L. Berg's decision to establish a separate subtribe for *Feijoa* was therefore unjustified. Burret (1941) investigated mature seeds of *F. sellowiana* (Berg) Berg (the type species of the genus) and concluded that the seeds were exalbuminous.

It seems from the literature that the quantity of endosperm which remains in mature seeds is variable and most probably not suitable as a diagnostic character. Our own observations indicate that the amount of endosperm in mature seeds of seed type X varies considerably. On the other hand, the amount of endosperm originally formed in the young seed is rather constant and more reliable for comparative purposes. We consider the limited formation of endosperm in seed type Y, compared with the abundant amount formed in seed type X, as taxonomically important.

5. Taxonomic Implications

5.1 Interspecific variation

Although not the principal aim of the present study, a few, possible interspecific differences in seed morphology have been noticed. These include the following: among the species with seed type X, *E. capensis* is clearly distinct from the others. It differs not only in having oblong-globose rather than subreniform seeds but also in having a testa which usually adheres to the pericarp. In species with seed type Y a clearly differentiated epidermal layer on the micropylar hemisphere of the mature testa has only been observed in *E. zeyheri* and *E. zuluensis*. However, much more material needs to be studied to ascertain the constancy of the latter feature.

5.2 Delimitation of *Eugenia* in southern Africa

Before evaluating the taxonomic status of species groups X and Y, the generic treatment of *Eugenia* in southern Africa will be reviewed briefly. Aspects regarding the taxonomic status of *Eugenia* and *Syzygium* in our area have previously been dealt with (Van Wyk *et al.* 1983) and will not be discussed in detail (see also Schmid 1972a).

Memecylon capense Ecklon & Zeyher (1836) was described from material gathered in the eastern Cape. Harvey (1838) provisionally refers two species from the Cape to the genus *Myrtus*? However, he suspects that his *Myrtus? capensis* is probably conspecific with *Memecylon capense* of which he had seen no authentic specimens. He was also not sure whether his putative *Myrtus* species were not in fact members of the genus *Jossinia*, which at that time was applied mainly to species from Madagascar and the Mascarenes. In the Addenda and Corrigenda of his work, Harvey confirms that his *M? zeyheri* belongs to *Eugenia*. He also says that *M? capensis* (of which he had seen no fruiting material) is, most probably, also a species of *Eugenia*. Sonder (1894) confirmed Harvey's suspicions and effected the new combination *E. capensis* (Eckl. & Zeyh.) Sond.

Dümmer (1912) lumped all the fleshy fruited Myrtaceae of southern Africa under *Eugenia s.l.* This view was not followed by most subsequent authors who tend to segregate *Syzygium* from *Eugenia s.l.* (for example Engler & Von Brehmer 1917; Engler 1921; Phillips 1951; Dyer 1975; White 1977, 1978). These, and many other authors accept unreservedly that *Eugenia* in southern Africa is congeneric with the mainly American *Eugenia s.str.*

5.3 Taxonomic status of species groups X and Y

The present study has shown that the development of seed types X and Y is significantly different. We consider these differences as fundamental and indicative of the taxonomic discreteness of species groups X and Y. In view of the many other characters which support the proposed grouping (Van Wyk 1978, Van Wyk *et al.* 1980; Van Wyk *et al.* 1982), we are convinced that two very natural groups of species are involved.

Work on the comparative morphology of the flower, inflorescence, fruit, bark and pollen is in progress and some of this work is already yielding additional support for the distinctness of the two groups of species. It is clear that species groups X and Y are more distantly than closely related. The resemblances between the two groups have probably resulted through convergence or parallel development from common ancestry. After a cursory examination of a rather limited number of tropical African species of *Eugenia* (unpublished data), we are inclined to suspect that most, if not all, African species can be disposed of in either of the proposed groups.

Species group X seems to be most closely related to the mainly New World species of *Eugenia*. For the present it is retained in this genus although it should perhaps be treated as a distinct section mainly on account of its polygamous nature and reduced number of ovules.

Species group Y does not seem to fit in satisfactorily with the present, rather vague concept of *Eugenia*. Its possible relationship with especially American eugenioid genera (notably *Myrcianthes* Berg and related genera — see McVaugh 1968) and the Old World genus *Jossinia*, needs further study although at this stage it does not seem to have any closely related counterparts outside Africa.

A number of Old World species (not southern African) were previously placed under *Jossinia* (De Candolle 1828; Blume 1849 – 51; Diels 1922; Merril 1950a & b). Kausel (1957b) also recognizes *Jossinia* and assigns it to his Plinioideae. In recent times, however, this genus has been included under *Eugenia* (Schmid 1972a & b; Scott 1980). *Jossinia*, at least in part, has also been recognized under *Eugenia* as a distinct subgenus (e.g. Baker 1877; Kostermans 1981) or section (Niedenzu 1893; De la Bâthie 1953). We are rather hesitant to merely accept the reduction of *Jossinia* to the synonymy of *Eugenia*. Many more features of the former group of Old World species need to be studied before a sound conclusion can be made.

Although not applied to southern African species, two additional generic names based on species from tropical Africa need to be considered. *Myrtopsis* O. Hoffm. (1881) and *Chloromyrtus* Pierre (1898) have each been proposed for a single African species *viz. M. malangensis* O. Hoffm. and *C. klaineana* Pierre. Both species were reduced to *Eugenia* by Niedenzu in 1893 and 1900, respectively. The combination *E. klaineana* (Pierre) Engl. was first used in Engler & Von Brehmer (1917, p.339). Following Amshoff (1958), Briggs & Johnson (1979) also include these two genera under *Eugenia*. It should also be noted that *Myrtopsis* Engl. (Rutaceae) has been conserved against *Myrtopsis* O. Hoffm. (Rickett & Stafleu 1959).

Considering the available data, we provisionally propose that species group Y be allocated generic rank. For the sake of nomenclatural stability, we have also considered subgeneric rank. However, such a decision would not be in accordance with traditional usage within the genus *Eugenia*. In the Myrteae much more work remains to be done in the field of generic concepts and it would be premature to pass final judgment on this issue. In the meantime efforts will be made to investigate more material from outside our area. A paper presenting a synthesis of all available evidence, including a definite decision on the taxonomic status of groups X and Y, is envisaged.

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