CONTRIBUTIONS TOWARDS A NEW CLASSIFICATION OF *EUGENIA* L. (MYRTACEAE) IN SOUTHERN AFRICA

by

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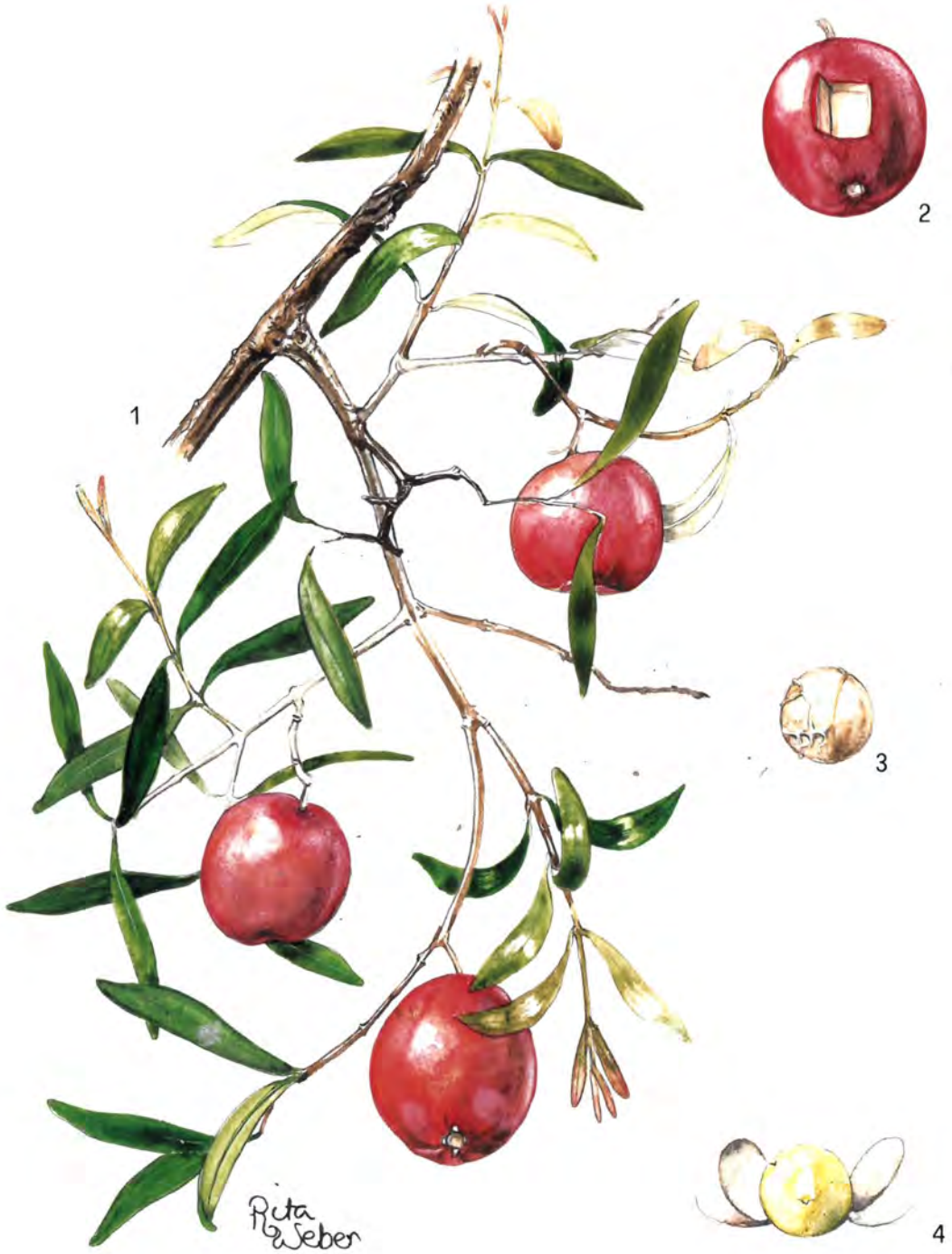
Eugenia umtamvunensis Van Wyk: 1, fruiting branch, x 1; 2, ripe fruit showing whitish flesh, x 1; 3, seed, x 2; 4, embryo, x 2.



Eugenia verdoorniae Van Wyk: 1, fruiting branch, ×1; 2, ripe fruit showing yellowish flesh, ×1; 3, seed, ×1; 4, seed with split-open testa—showing the embryo, ×1.

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Chapter 1

INTRODUCTION

The Myrtaceae is a large, well defined family of about 147 genera and more than 3 650 species (Schmid 1980). It is traditionally divided into two well marked but evidently allied subfamilies, namely the Myrtoideae and the Leptospermoideae. The majority of the succulent-fruited Myrtoideae occur in central and South America, whereas the capsular-fruited Leptospermoideae is best developed in Australasia.

Eugenia L. is one of about 70 genera belonging to the Myrtoideae. It was founded by Linnaeus (1753) and named in honour of Prince Francois Eugène de Savoie-Carignan (1663–1736). Concepts and circumscriptions of *Eugenia* have varied over the years. For a general discussion of generic concepts in the Myrtoideae, including the delimitation of *Eugenia*, McVaugh (1968) may be consulted. At times *Eugenia s.l.* has been treated as an immense collective genus, including amongst others the large genus *Syzygium* Gaertn. Schmid (1972) estimated that nearly 70 generic names have been used for various species of *Eugenia s.l.* Evidence, however, has been accumulating in recent years that *Syzygium* and some closely related small genera (e.g. *Acicalyptus* A. Gray, *Aphanomyrtus* Miquel, *Cleistocalyx* Blume and *Jambosa* DC.) are quite different from *Eugenia s.str.* as lectotypified by *E. uniflora* L. For a review of the *Eugenia–Syzygium* controversy, see Schmid (1972).

Eugenia in the strict sense is still an extremely large genus of about 1 000 species. The majority of these occur in central and South America. Particularly in some wet forests of southern Bahia, eastern Brazil, the Myrtoideae (including many eugenias) is the dominant group in terms of number of species, number of individuals and in total basal area (Mori *et al.* 1983). Relatively few species of *Eugenia s.str.* are present in Africa and the rest of the Old World. In Asia it is largely replaced by *Syzygium.*

A critical monographic revision of *Eugenia* has not yet been attempted. *Eugenia* represents the generalized type of the eugenioid Myrtaceae with no special morphological features. The species are distressingly alike in aspect and in most individual characters, making identification and classification of the species a difficult and tedious task. Leaves are essentially all opposite and entire with brochidodromous venation. The inflorescences are of a few basic types and the flowers are all rather similar. It has for example become almost customary to identify specimens of *Eugenia* from particularly tropical America only to the genus.

The number of species of *Eugenia s.str.* in Africa is estimated at about 50. In this part of the world the generic limits between *Eugenia* and *Syzygium* are distinct, thereby militating against the unification of the two genera (Van Wyk 1978). *Eugenia* has nevertheless been treated in a wide sense in some old taxonomic accounts, e.g. Lawson (1871) and Duemmer (1912). The last attempt to give a review of the African species of *Eugenia s.str.* is the brief and now outdated account by Engler (1921). A number of regional studies of *Eugenia* in Africa have subsequently been published. These, like all previous studies of the African members, were usually based on limited numbers of herbarium specimens. Moreover, evidence for taxonomic decisions was based on macromorphological features (particularly those of the leaf) only.

Both *Syzygium* and *Eugenia* were maintained by Sonder (1862) in his account of Myrtaceae for Flora Capensis. He recognized five species and two varieties of *Eugenia* in southern Africa. At that stage many species were still undiscovered and only 11 herbarium collections were cited.

Duemmer (1912) provided the first comprehensive treatment of *Eugenia* in southern Africa. He distinguished 13 species, three of which are now classified in *Syzygium* (Table 1, page 175). Within the 10 species of *Eugenia s.str.* he also recognized six varieties. Duemmer's account was prepared from about 44 collections available at Kew and the British Museum. Although many of the species proposed by Duemmer were based on one or a few specimens each, many of his taxonomic judgements proved to be sound and are still upheld today (Van Wyk 1978).

Recently a taxonomic revision of *Eugenia* for Flora Zambesiaca (FZ) was extended to include all the southern African species (White 1977, 1978). Within the Flora of Southern Africa (FSA) region, White took the drastic action of reducing the number of species to two, viz. *E. capensis* (Eckl. & Zeyh.) Sond. and *E. erythrophylla* Strey (Table 1; page 175). *E. capensis* is the only one of the 10 species proposed by Duemmer that is being retained at the species level, while *E. erythrophylla* was fairly recently described by Strey (1972). White considered *E. capensis* to be a polytypic species with at least nine subspecies recognizable in southern Africa south of Tan-

zania and the Congo basin. Six subspecies are confined to the FSA region, with two of these extending northward into the FZ area in southern Mozambique. Although White's classification has subsequently been uncritically adopted by some workers (e.g. Coates Palgrave 1977), it has not yet received wide support. In his proposed classification White, like others before him (e.g. Harvey 1838; Sonder 1862; Engler 1899; Duemmer 1912; Engler & Von Brehmer 1917; Engler 1921; Amshoff 1958), relied mainly upon macromorphological characters, particularly leaf shape. He had, however, much more herbarium material at his disposal, as well as the advantage of seeing many of the taxa in the field during his extensive travels in Africa.

My own work on the southern African species of *Eugenia* was initiated in 1975. At that stage considerable confusion about the delimitation of the native taxa existed. What seemed to be undescribed species and misidentified specimens abounded in herbaria. A reinvestigation of the group therefore appeared desirable. The main objective of the study was to provide a taxonomic account for the FSA. At first the variation encountered in macromorphological features seemed to be confusing and it was decided to explore some alternative sources of taxonomic evidence as a possible aid towards solving the difficulties. Only after the study was well under way, I learned of the revision that was in progress for FZ. In view of the different approach followed, and realizing that already at that stage there were differences in our treatment of the genus, it was decided to proceed independently with the project.

The results of an anatomical study of the leaf lamina and stem of southern African members of *Eugenia* were presented in the form of an M.Sc. thesis (Van Wyk 1978). Both quantitative and qualitative anatomical characters were evaluated for their taxonomical significance. A numerical analysis based on 100 anatomical leaf and stem characters supported the distinctness of many of the traditionally accepted species, thereby particularly agreeing with the classification of Duemmer (1912). A number of characters were found to support the separation of the species into two distinct supraspecific groups, provisionally designated groups X and Y. Practically, the most useful of these is the position in which the first-formed periderm originates in the stem. The identity of species with a vague taxonomic position could be ascertained by checking the position of the periderm in the type specimens (Van Wyk 1978; Van Wyk *et al.* 1980; page 76).

The unexpected discovery that at least on anatomical grounds *Eugenia* in the FSA region constitutes a heterogeneous taxon, gave rise to many questions. For example: Would this division be supported by evidence from other sources, particularly macromorphology? Would the distinctions between the groups hold for species from outside the FSA region? Are groups X and Y natural or artificial categories? To what formal taxonomic rank should the groups be allocated? Are we not perhaps dealing with two distinct genera? These and other unanswered questions called for more studies on the native taxa and comparisons with particularly eugenioid genera in other parts of the world, before a formal taxonomic revision could be proposed.

The present account is an extension of the work presented in Van Wyk (1978). Various additional sources of potential taxonomic evidence were studied in the light of the new taxonomic framework suggested by the anatomical findings. Some questions were answered, but the work also gave rise to many new ones. This is still not the final revision, although it may be considered a step closer to the eventual goal. It is hoped that this comprehensive study will not only contribute towards a better understanding of the local taxa, but also provide guidelines for similar studies on members of *Eugenia* in other parts of the world.

This thesis consists of a collection of contributions on several diverse aspects of *Eugenia* in southern Africa. These studies were all approached with the primary objective of a taxonomic revision in mind. Contributions are in the form of papers (reprints or copies thereof) which have been published regularly in various scientific journals over a period of about seven years. A paper on the reproductive biology of *Eugenia* is included in manuscript format. The paper on the structure and taxonomic value of the first-formed stem periderm (Van Wyk *et al.* 1980; page 76) is the only one largely based on results put forth in Van Wyk (1978). It has nevertheless been included because of its relevance to the paper on bark structure (Van Wyk 1985; page 99). Details of materials and methods, references etc. are presented in the individual contributions. In most papers a comprehensive discussion of the results is presented. A synthesis of the principal findings of the work up to now, as well as an outline of a provisional new classification of the native species of *Eugenia* is presented under 'General Discussion' in Chapter 10, page 172. This is followed by keys to the species and subspecies of *Eugenia* in the FSA region, and notes on diagnostic characters, geographical distribution, typification and synonymy (Chapter 11; page179). It should be stressed that this is not the formal revision yet, but it is presented to serve as a guide to the author's concept of the taxa mentioned in the various papers. A list of publications to which reference has been made in those parts of the text *other* than the reprints/manuscript of papers, is presented at the end of each chapter.

The papers presented here show some stylistic irregularities. These are primarily due to differences in layout and style required by the various journals. To get manuscripts accepted for publication, conformation to some idiosyncrasies of referees and editors was sometimes unavoidable. The published papers contain a good number of minor typographic errors. Many of these appeared anew or were not rectified between the time proofs left my hands and the time of printing. Most of the errors were corrected on the enclosed reprints. The thesis is nevertheless provided with an Appendix (page 236) for corrections and additional notes. Since the publication

of some of the papers my ideas have undergone some relatively minor changes. In some cases new information with a bearing on the contents of a paper was found. This is also noted in the Appendix.

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CHAPTER 2

STRUCTURE AND TAXONOMIC VALUE OF STOMATA

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The genus *Eugenia* L. (Myrtaceae) in southern Africa: the structure and taxonomic value of stomata

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The mature stomatal morphology of 11 southern African species of *Eugenia*, and also of *E. uniflora* L. (naturalized) and *E. incerta* Dümmer (a garden plant of unknown origin) has been studied by light and scanning electron microscopy.

Leaves of all the species are hypostomatic and water-stomata are occasionally present. Two different stomatal types, X and Y, differing mainly in their cuticular ornamentation, were found in the southern African species. The grouping of species based on stomatal characters supports a previous grouping of species on the basis of periderm and seed characters.

Conspicuous lipid bodies, usually present in the subsidiary cells, are limited to the southern African species. Although the subsidiary cells do not differ in shape and size from adjacent epidermal cells, their contents often have a higher tannin content than ordinary epidermal cells. The variable patterns of arrangement of the three to five subsidiary cells makes it difficult to identify the stomata with existing classifications based on mature topography. Thus, a new term 'anomostaurocytic' is proposed for the stomatal type found in the southern African species.

Stomata of *E. uniflora* and *E. incerta* are paracytic and anomocytic respectively, and the cuticular ornamentation of their stomata differs from those of the southern African species. The view that *E. incerta* is not closely related to the southern African species is supported by differences in its cuticular ornamentation, lack of lipid bodies in the subsidiary cells, anomocytic stomata and prominent T-pieces at the guard cell poles.

KEY WORDS:—epidermis – *Eugenia* – lipid body – Myrtaceae – stomata – subsidiary cell.

CONTENTS

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INTRODUCTION

The use of stomatal characters as taxonomic criteria at various levels of the taxonomic hierarchy is well established in comparative anatomical, phylogenetical and palaeobotanical studies. However, little use has been made of such characters for taxonomic problems in the Myrtaceae.

In an anatomical study which included representatives of various genera of the Myrtaceae, Lignier (1887) came to the conclusion that although the arrangement of stomata on mature leaves varies according to the species, the first divisions in the ontogeny of the stomata are invariably the same. Statements by Solereder (1908) referring to the structure of the stomata of the Myrtaceae, are essentially based on the treatise of Lignier (1887) and describe the mature stomata as being either devoid of subsidiary cells, or accompanied by two such cells parallel to the guard cells. According to Metcalfe & Chalk (1950), stomata devoid of subsidiary cells are those most frequently encountered in the family.

Bandulska (1931) investigated the cuticular anatomy of some Recent and fossil members of *Tristania* and *Rhodomyrtus* and clearly showed the utility of stomatal characters in the systematics of these genera. More recently Carr, Milkovits & Carr (1971) and Carr & Carr (1976a, b, 1978, 1979) noted that the stomata of certain *Eucalyptus* species have species-specific features that can be regarded as diagnostic.

As far as we have ascertained, stomatal features apparently have not been applied to taxonomic problems in the large and complex genus *Eugenia*. However, Ferri (1971), in a paper primarily dealing with transpiration in the Myrtaceae, described the mature stomata of *E. brasiliensis* Lam. as anomocytic and those of *E. tomentosa* Camb. and *E. uniflora* L. as paracytic, and by implication indicated possible interspecific differences.

The aim of this paper is to investigate the taxonomic potential of stomatal features in some southern African species of *Eugenia*.

MATERIAL AND METHODS

The following species indigenous to southern Africa were examined:
Eugenia albanensis Sonder
E. capensis (Ecklon & Zeyher) Sonder
E. erythrophylla Strey
E. cf. *mossambicensis* Engl.
E. natalitia Sonder
E. pusilla N. E. Br.
E. simii Dümmer
E. verdoorniae Van Wyk
E. woodii Dümmer
E. zeyheri Harvey
E. zuluensis Dümmer

Material from *E. uniflora* L. (naturalized in parts of Natal) and *E. incerta* Dümmer (described from a cultivated plant of unknown origin in the Durban Botanical Gardens and probably not indigenous) was also examined and compared with the native taxa. Voucher specimens are listed in the Appendix.

Most material was freshly collected, fixed and stored in FAA. Prior to fixation,

Table 1. Maximum guard cell dimensions: stomatal type X

Species	Anticlinal diameter (μm)	Periclinal diameter (μm)	Length of stomatal ledges (μm)
Eugenia capensis	8.0–11.0	10.0–10.4	3.4
E. cf. *mossambicensis*	7.0–8.0	8.0	2.3
E. natalitia	4.6–6.0	6.8–8.0	1.7–2.3
E. simii	4.6–6.0	6.8–9.8	1.7–2.3

dried leaves from herbarium specimens were first rehydrated in boiling water. The material was then thoroughly washed in water to remove all traces of fixative.

For light microscopy, transverse sections of mature leaves were prepared according to the methods used by Van Wyk, Botha & Coetzee (1980). Mounts of epidermal peels and cuticular membranes were obtained respectively by the $CuSO_4 \cdot 5H_2O$/HCl method (Ram & Nayyar, 1974) and after maceration with Jeffrey's solution (Stace, 1965; Kiger, 1971). Cuticle preparations were stained with safranin O (Johansen, 1940) and epidermal peels with safranin O or toluidine blue.

Histochemical tests for lipids were made on epidermal peels and fixed sections or paradermal sections of fresh leaves. Material was also stained in a saturated and filtered solution of Sudan III, Sudan IV and Sudan Black B in 70% ethanol for about 20 min, and mounted in glycerine-gelatin (Jensen, 1962).

Standard procedures were followed for SEM. Leaf fragments were infiltrated with liquid CO_2 and dried in a Bomar SPC-900/EX critical point drier, sputter-coated with gold and viewed with a Phillips PSEM 500 microscope.

The anticlinal and periclinal diameters of guard cells were calculated by measuring the maximum distance between the inner and outer, and poral and epidermal walls respectively on transverse sections (terminology according to Stace, 1965).

Measurements of the width of the stomatal ledges (Fig. 1) were taken in two different ways: (a) the maximum width of the free part of the stomatal ledge—in all the species with stomatal type X; and (b) the maximum width as measured from the outer edge of the outer wall of the guard cell and the end of the stomatal ledge—in all species with stomatal type Y.

All measurements were taken from stomata sectioned transversally at right angles to, and more or less through the middle of, the longitudinal axes of the

Table 2. Maximum guard cell dimensions: stomatal type Y

Species	Anticlinal diameter (μm)	Periclinal diameter (μm)	Length of stomatal ledges (μm)
Eugenia albanensis	10.0–11.4	10.3–12.5	4.6–6.8
E. erythrophylla	12.0–15.0	12.0–15.0	11.4–22.8
E. pusilla	10.0	10.4	6.8
E. verdoorniae	6.8–8.0	10.3–11.4	4.2–5.7
E. woodii	8.0	10.3	6.0
E. zeyheri	10.0	10.3	5.0–6.0
E. zuluensis	10.0–11.0	11.4–12.0	3.4–5.7

guard cells. Water-stomata were excluded. Five stomata per leaf from each of the specimens mentioned in the Appendix, excepting those with an asterisk, were measured. The figures in Tables 1 and 2 are the ranges of maximum values for each species.

Reference to the epidermal cells and cuticular membrane will be limited mostly to features associated with the stomatal-complex. The descriptive terminology will be based mainly on that of Stace (1965) and Metcalfe & Chalk (1979).

RESULTS

Stomata of the southern African species

Leaves of all species are hypostomatic. Stomata are dispersed randomly over the whole abaxial surface except the midrib and in the vicinity of the subepidermal secretory cavities. Although the secondary and higher order venation of the leaves is not usually visible from the outer surface of the lamina, it occasionally reaches close to the abaxial epidermis. On such leaves the stomata tend to be confined to the poorly defined areolae.

When viewed with the SEM, the stomata appear elliptic to circular in outline. The guard cell pairs are level with, or slightly sunken below the epidermis. Their long axes are randomly orientated. In surface view the guard cells are reniform and usually elliptic (Figs 21, 27, 29). The stomatal apertures open into prominent sub-stomatal cavities. Most of the stomata from one leaf are more or less the same size.

Abnormally large water-stomata are often present, differing from typical stomata in their cuticular ornamentation (Figs 2–4, 12, 21, 29).

The guard cells are surrounded by three to five (rarely more) subsidiary cells, of which one or more is occasionally shared by adjacent stomata. Although these cells show no specific pattern of arrangement around the guard cells, they usually differ conspicuously from adjacent epidermal cells by their contents which stain more intensely with safranin O and toluidine blue. This can probably be attributed to the denser and more granular cytoplasm and, in many specimens, a much higher tannin content than in ordinary epidermal cells (Figs 22, 23). However, the most

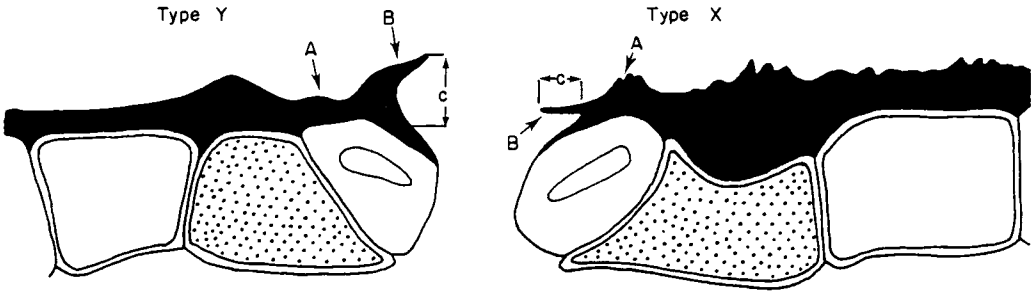


Figure 1. Schematic presentation of a stoma with one half belonging to type X and the other to type Y, showing the nature and position of the stomatal ridge (A) and ledge (B) in transverse section and the width of the stomatal ledge as measured in the two stomatal types (C).

conspicuous feature of the subsidiary cells is the presence of usually one spherical lipid body (probably an oil droplet or elaioplast) in the cytoplasm of each cell. These lipid bodies are usually absent from ordinary epidermal cells, or if present, much smaller than those in the subsidiary cells. Very rarely is there more than one per cell, although up to three have been observed. They do not stain with safranin O and toluidine blue. Intense staining was obtained with the lipid dyes Sudan III, Sudan IV and Sudan Black B. The size of the lipid bodies varied from very small (or absent in young leaves) to a rather uniform maximum diameter of 5–10 μm in the subsidiary cells of mature leaves (Figs 18, 22–26).

The outer surface of the cuticular membrane usually follows the contour of the epidermal cells, except in leaves with thick cuticles where the surface is more even. Above the subsidiary cells the cuticular membrane is thicker and notably raised—thus rendering their positions visible in stained cuticular preparations (Figs 6, 16, 17). The subsidiary cells often bulge slightly below the guard cells into the substomatal cavity, appearing somewhat similar to inner stomatal ledges (Fig. 1).

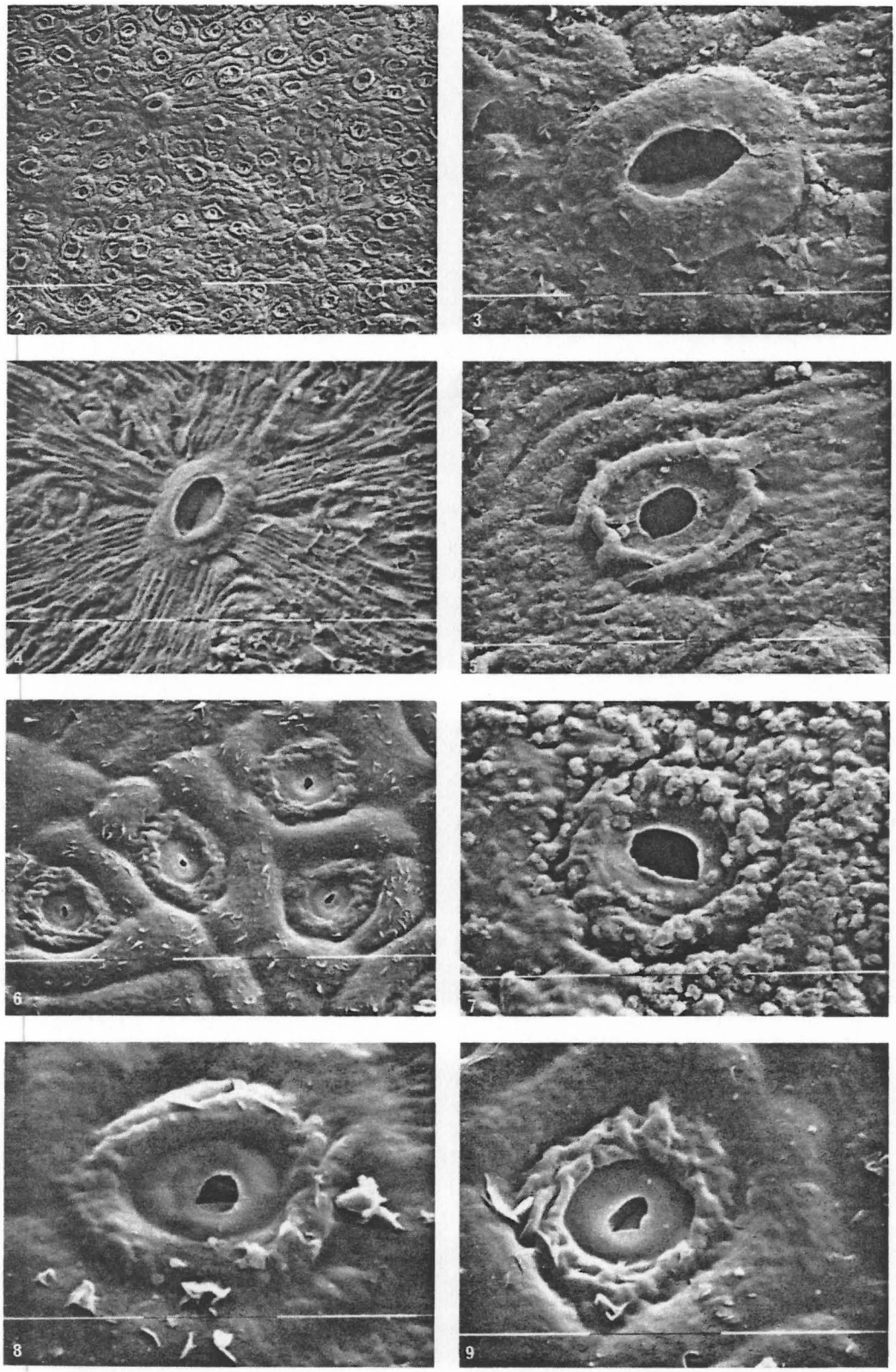
The cuticular membrane covering the subsidiary and guard cells, penetrates the pore up to the inner walls of the guard cells (Figs 20, 28). Above the guard cells the cuticular membrane is protracted into a pair of more or less continuous outer stomatal ledges (Fig. 1), forming a front (epistomatal) cavity. In some specimens the front cavity of some stomata is plugged with a resinous mass (Fig. 19). In addition, an elevated cuticular ridge, situated on top of each guard cell, surrounds the ledge. Here we call it the stomatal ridge (Fig. 1). The detailed patterning of guard cell cuticular ornamentation varies according to species and was found to be of taxonomic value. From this character, two stomatal-types, X and Y, are distinguished and described in detail below.

Stomatal type X

Stomatal type X (Figs 1–9, 18–21, 30, 31) is characterized by stomatal ledges which are more or less horizontally aligned with the leaf surface. The prominent, more or less circular stomatal ridge, is situated approximately opposite the ridge (or outermost point) of the outer guard cell wall (Figs 1, 20, 30, 31). The outer surfaces of the stomatal ridges are usually conspicuously wrinkled and both the ridges and ledges are usually continuous between the guard cells without reflecting the position of the common cell wall between these cells (Figs 5–9).

The subsidiary cells of type X stomata contain less tanniniferous substances and their outer periclinal walls are more sunken than those of type Y. As a result the cuticular membrane of type X stomata is thicker above the subsidiary cells, although not as prominently raised above the surface of the lamina as in type Y stomata (Figs 20, 30, 31). The cuticular membrane often shows conspicuous striations above the subsidiary cells and other epidermal cells (Figs 4, 5, 20).

Stomatal type X occurs in the following species: *E. capensis* (Figs 2–5, 20, 30); *E. natalitia* (Figs 8, 31); *E. simii* (Figs 6, 9), and *E.* cf. *mossambicensis* (Fig. 7). No constant qualitative differences have been found between these species. Waterstomata are often present and are especially prominent in specimens of *E. capensis* (Figs 2–4, 21) and the cuticular ornamentation differs from that of ordinary stomata. The epicuticular wax layer varies from specimen to specimen and is apparently of no taxonomic significance. The stomatal frequency is variable,



ranging from (300) 400–700 (1000) mm^{-2}. Dimensional variation is given in Table 1.

Stomatal type Y

Stomatal type Y (Figs 1, 10–17, 22–29, 32, 33) is characterized by stomatal ledges of which the alignment is more or less perpendicular to the lamina surface. The stomatal ledges are situated opposite the ridge of the outer guard cell walls, corresponding to the position occupied by the cuticular ridges in type X stomata (Figs 1, 32, 33). As clearly illustrated in *E. erythrophylla*, the cutinized outer wall of the guard cells often stretches for some distance into the stomatal ledge (Fig. 32). A smooth surfaced stomatal ridge surrounds the ledges (Figs 13–15, 17). Although in surface view the counterparts of both these cuticular structures are more or less continuous between the two guard cells, a slight depression is usually present where the guard cells meet (especially between the stomatal ledges). Stomatal shape as shown in surface view (Figs 13, 14) tends to be elliptic to oval by cuticular ornamentation rather than circular as in type X.

The tanniniferous contents of the subsidiary cells stain much more intensely than those of adjacent epidermal cells. The cuticular membrane covering the subsidiary cells is smooth-surfaced (thicker than above ordinary epidermal cells) and often conspicuously raised above the surface of the lamina (Fig. 17).

Stomatal type Y occurs in *E. albanensis*, *E. erythrophylla*, *E. pusilla*, *E. verdoorniae*, *E. woodii*, *E. zeyheri* and *E. zuluensis*. Although no distinct qualitative interspecific differences were found, the stomatal ridge tends to be poorly developed, or absent in specimens of *E. erythrophylla* (Figs 10, 11, 32). However, it is possible that the presence of the ridge is obscured by the exceptionally thick cuticular membrane in this case. Water-stomata are occasionally present (Figs 12, 21). The epicuticular wax layer shows great variation between specimens (Figs 16, 17). Stomatal frequency tends to be lower than in specimens of type X, ranging from (100) 200–400 (700) mm^{-2}. Dimensional variation is given in Table 2.

Stomatal features of E. uniflora *and* E. incerta

Both species are hypostomatic. The stomata are randomly scattered in the areolae which are more clearly defined than those of the indigenous species. The cuticular membrane ends where the poral and inner walls of the guard cells meet, as in the indigenous species (Fig. 41).

Surface ornamentation as viewed with the SEM is shown in Figs 34 & 38 and differs conspicuously from that of the indigenous species. No lipid bodies have been observed in the epidermal cells of either species (Figs 37, 39).

Subsidiary cells usually more tanniniferous than ordinary epidermal cells occur in *E. uniflora*. Most stomata have two subsidiaries lying parallel to the guard cells

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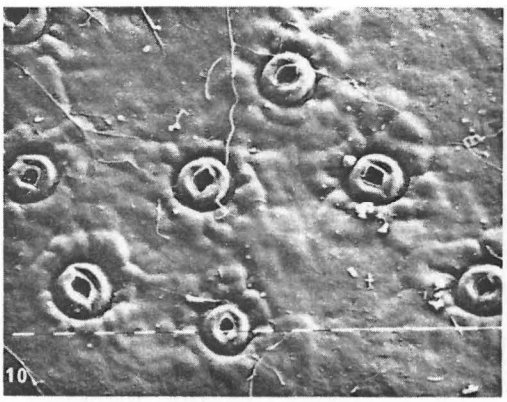
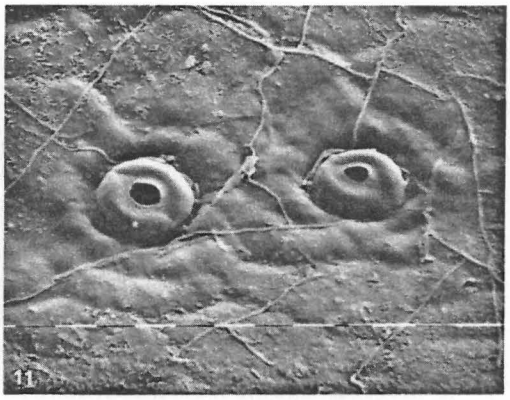
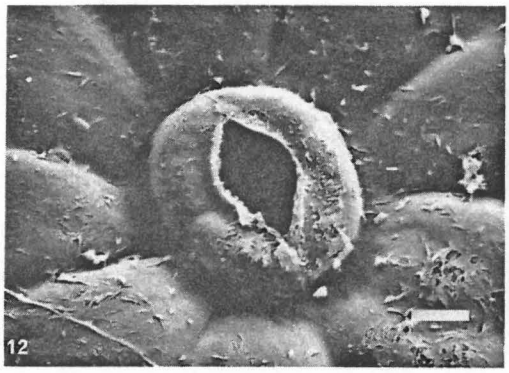
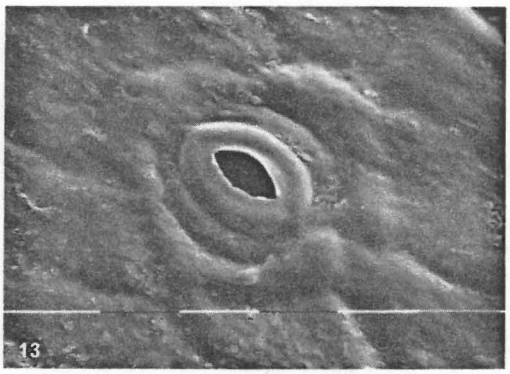
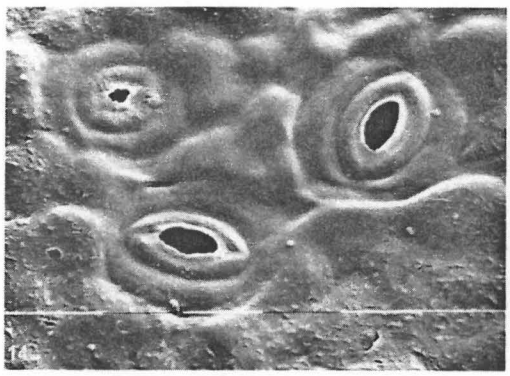
Figures 2–9. SEM micrographs to show the morphology of stomatal type X. Fig. 2. *Eugenia capensis*, abaxial lamina surface showing two water-stomata and typical type X stomata. Fig. 3. *E. capensis* (*Van Wyk, 1262*), water-stoma. Fig. 4. *E. capensis* (*Van Wyk, 987*), water-stoma—note cuticular striations. Fig. 5. *E. capensis* (*Van Wyk, 1262*), stoma. Fig. 6. *E. simii* (*Van Wyk, 1680*), abaxial lamina surface, note wrinkled stomatal ridges and raised cuticular membrane above subsidiary cells. Fig. 7. *E.* cf. *mossambicensis* (*Kruger, 305*), stoma. Fig. 8. *E. natalitia* (*Van Wyk, 1701*), stoma. Fig. 9. *E. simii* (*Van Wyk, 1664*), stoma. Scale: 1 segment of scale-line = 100 μm (Fig. 2) or 10 μm (Figs 3–9).

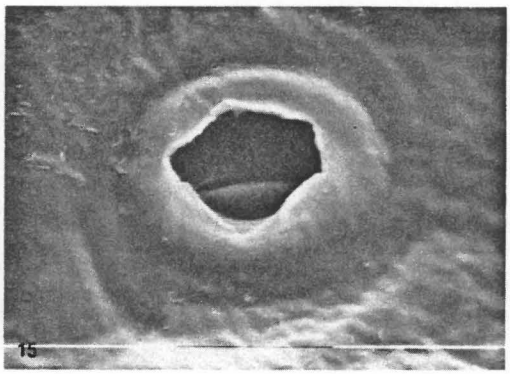


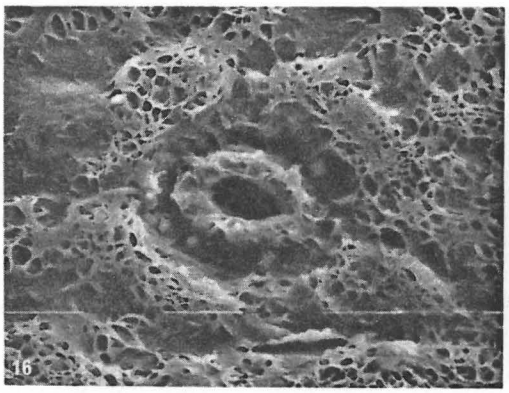


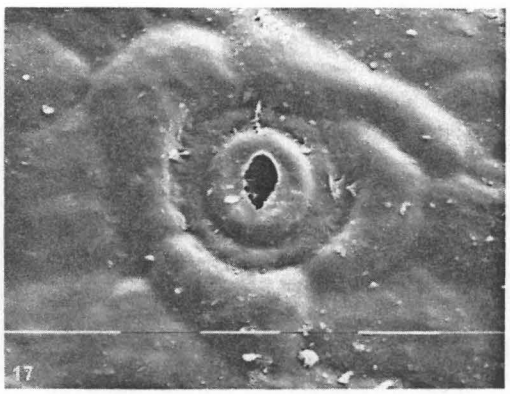


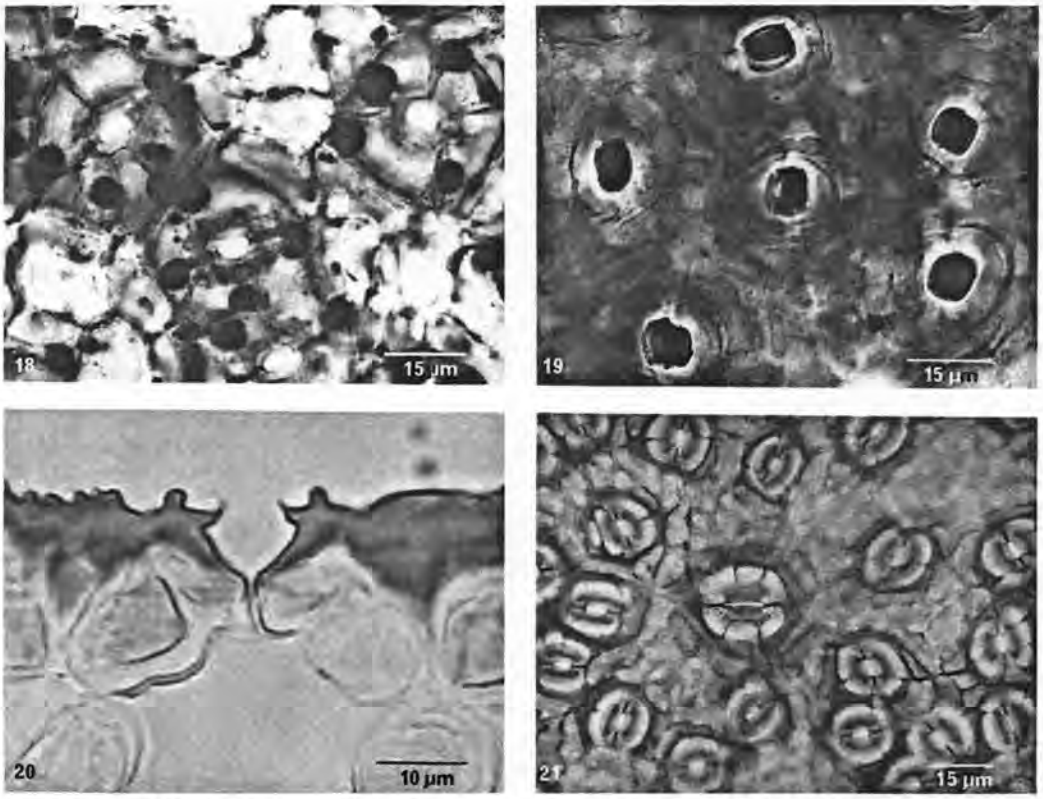












Figures 18–21. Light micrographs to show the morphology of stomatal type X. Fig. 18. *Eugenia capensis* (*Van Wyk, 4226*), abaxial epidermis stained with Sudan Black B, showing stained lipid bodies in subsidiary cells. Fig. 19. *E. capensis* (*Van Wyk, 4226*), unstained epidermis showing stomata with front cavities plugged with a resinous mass. Fig. 20. *E. capensis* (*Van Wyk, 4226*), transverse section of stoma stained with Sudan Black B and showing position of cuticular membrane. Fig. 21. *E.* cf. *mossambicensis* (*Van der Schijff, 3751*), safranin-stained cuticular preparation showing a single water-stoma.

(Figs 35, 37), although up to four may occur (Fig. 36). In the latter case the aberrant stomata tend to be confined to small, localized areas on the lamina.

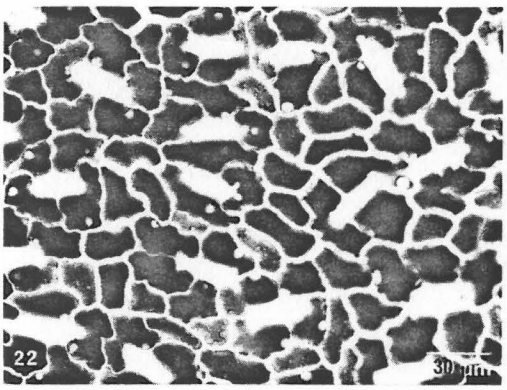
No distinct subsidiary cells have been observed in *E. incerta* (Fig. 39). Prominent T-pieces at the stomatal poles are present and show up particularly well in preparations stained with Sudan Black B (Fig. 40).

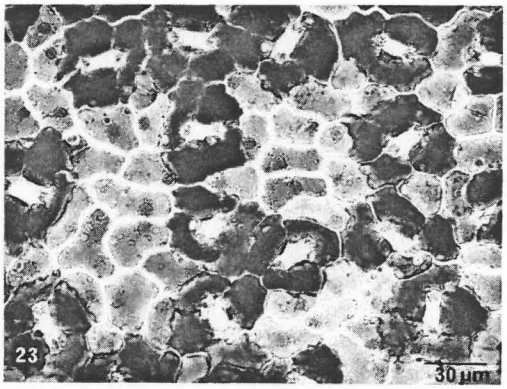
DISCUSSION

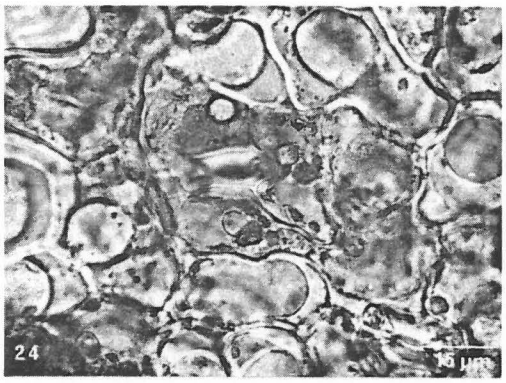
Stomatal morphology

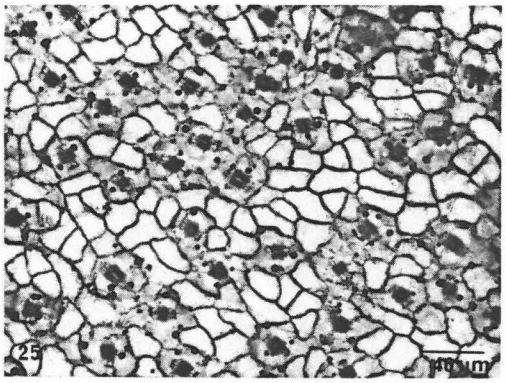
The observations recorded in this study pose two basic, although somewhat problematic, questions regarding stomatal morphology: are the epidermal cells

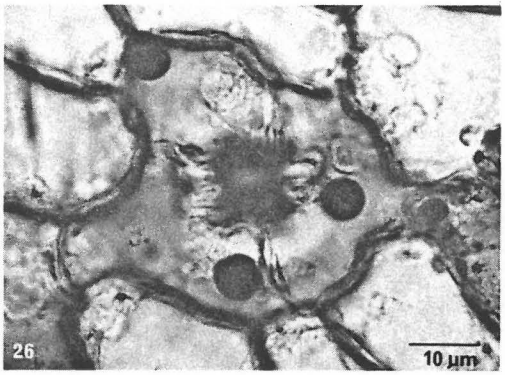
Figures 10–17. SEM micrographs to show the morphology of stomatal type Y. Fig. 10. *Eugenia erythrophylla* (*Van Wyk, 1548*) abaxial lamina surface showing stomata. Fig. 11. *E. erythrophylla* (*Van Wyk, 1583*) stomata—note poorly developed stomatal ridge and epiphyllous fungal hyphae. Fig. 12. *E. erythrophylla* (*Van Wyk, 1543*), actinocytic water-stoma. Fig. 13. *E. zuluensis* (*Van Wyk, 1248*), stoma. Fig. 14. *E. woodii* (*Van Wyk, 825*), stomata—note elliptic shape. Fig. 15. *E. pusilla* (*Forbes, 6350*), stoma. Fig. 16. *E. verdoorniae* (*Van Wyk, 1622*), stoma. Fig. 17. *E. verdoorniae* (*Van Wyk, 1616*), stoma—note variation in nature of epicuticular wax layer by comparing with Fig. 16. Scale: 1 segment of scale line = 10 µm.

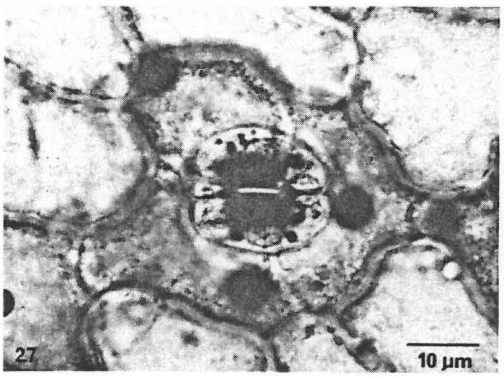


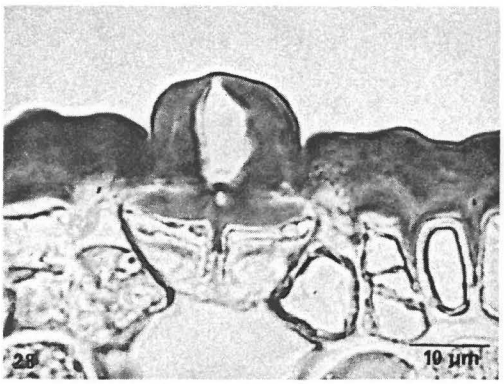


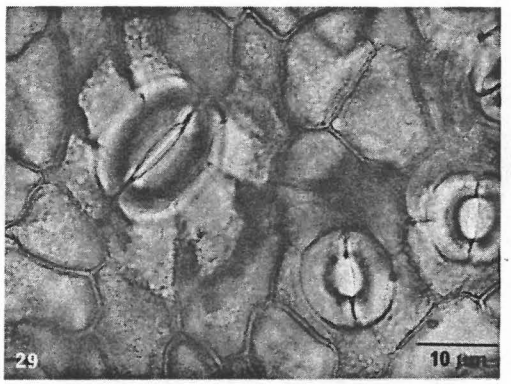


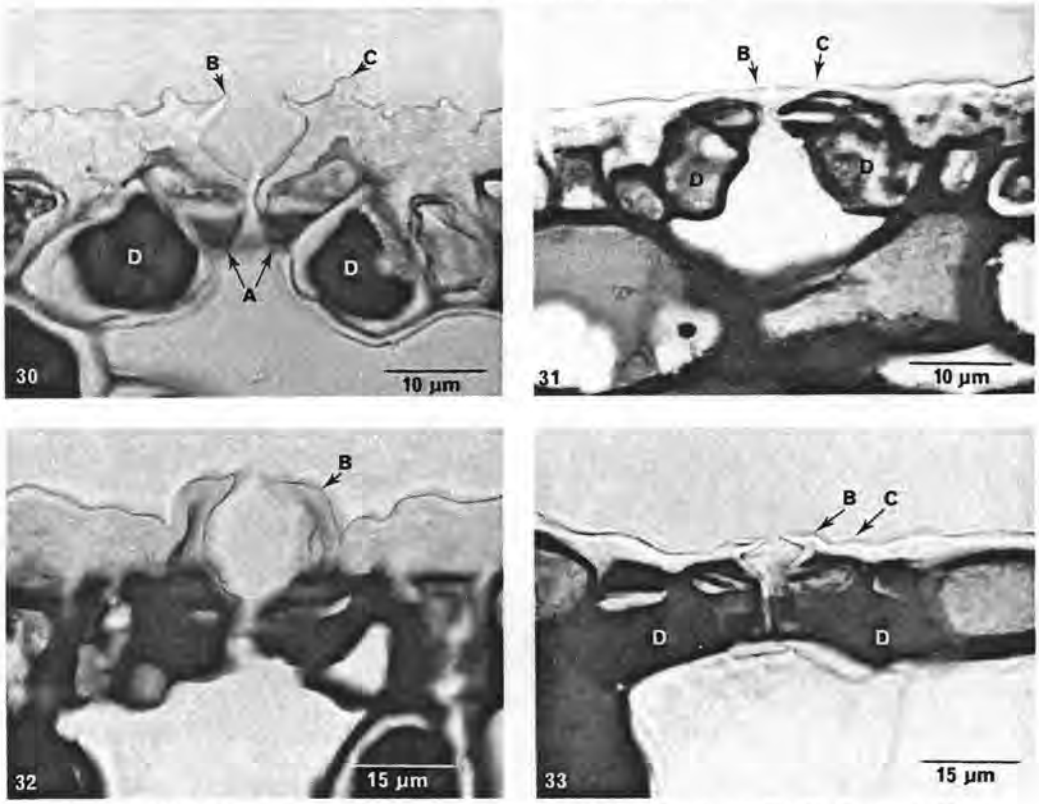










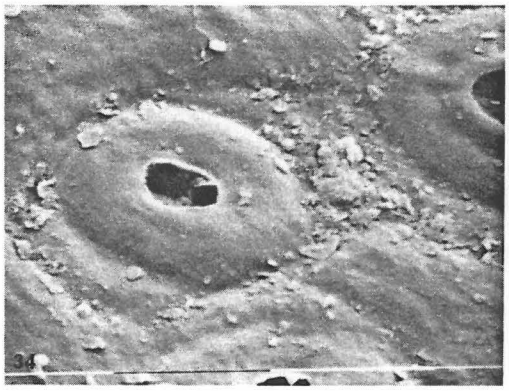


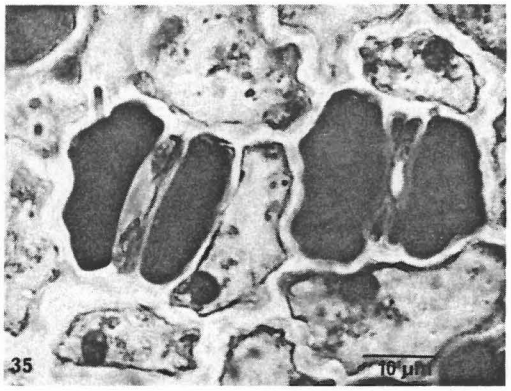
Figures 30–33. Transverse sections of stomata of southern African *Eugenia* spp. Fig. 30. *E. capensis* (*Van Wyk, 1262*). Fig. 31. *E. natalitia* (*Van Wyk, 1701*). Fig. 32. *E. erythrophylla* (*Van Wyk, 1698*). Fig. 33. *E. albanensis* (*Van Wyk, 1342*). A, Guard cells; B, stomatal ledges; C, stomatal ridges—not conspicuous in Figs 31 & 33 and apparently absent in Fig. 32; D, subsidiary cells.

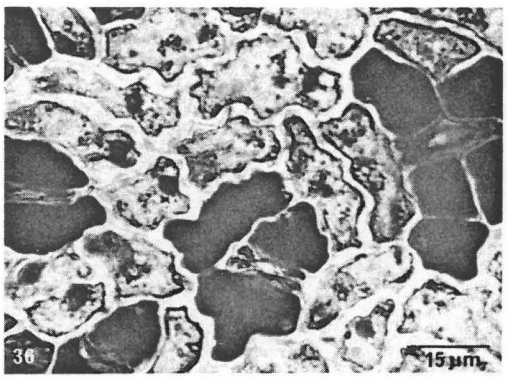
surrounding the stomata sufficiently modified as to be regarded as subsidiary cells; and to which stomatal type should the stomatal complex of the investigated species belong?

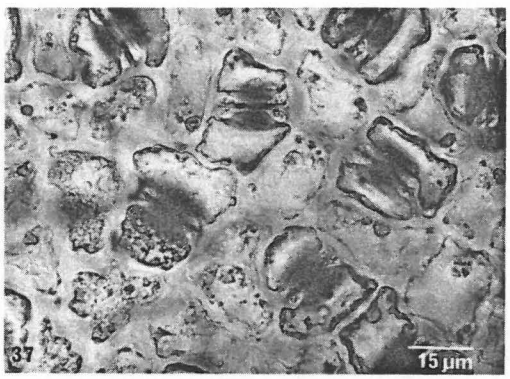
Concerning the former question, the widely quoted definitions of subsidiary cells, which apparently do not take into account the composition of the cell contents, prove to be vague and inadequate to comply with the question. The indiscriminate use of the term 'subsidiary cell' is discussed by Patel (1978), who comes to the conclusion that subsidiary cells must differ morphologically and physiologically from other epidermal cells. As the physiology of these cells may be reflected by their morphology, histology and biochemistry, he listed a number of chemical tests for their identification. The fact that subsidiary cells can sometimes be distinguished readily from adjacent living epidermal cells by their contents,

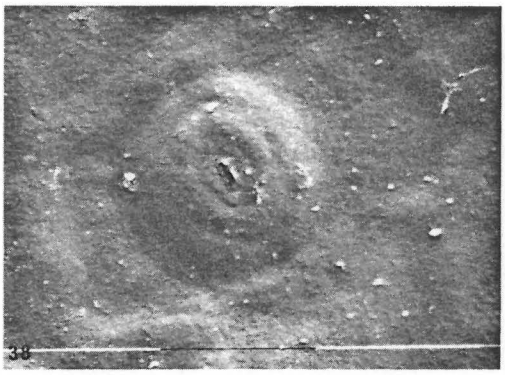
Figures 22–29. Light micrographs to show the morphology of stomatal type Y. Fig. 22. *Eugenia albanensis* (*Van Wyk, 1613*), epidermis stained with toluidine blue, showing unstained lipid bodies. Fig. 23. *E. albanensis* (*Van Wyk, 1690*), safranin-stained epidermis showing tanniniferous subsidiary cells with unstained lipid bodies. Fig. 24. *E. verdoorniae* (*Van Wyk, 4225*), unstained epidermis showing single lipid body and nucleus in each subsidiary cell. Figs 25–26. *E. verdoorniae* (*Van Wyk, 4225*), epidermis stained with Sudan Black B, showing stained lipid bodies in subsidiary cells. Fig. 27. *E. verdoorniae* (*Van Wyk, 4225*), guard cells. Fig. 28. *E. erythrophylla* (*Van Wyk, 1698*), transverse section of stoma stained with Sudan Black B. Fig. 29. *E. albanensis* (*Ward, 4530*), safranin-stained cuticular membrane showing a water-stoma.

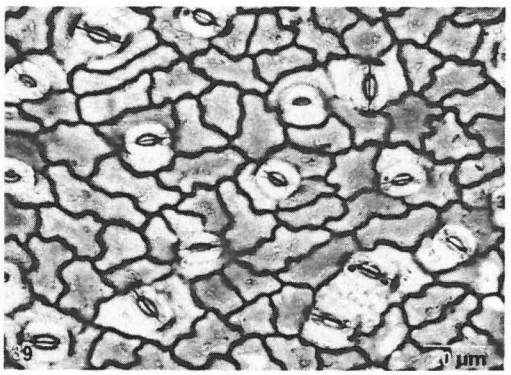


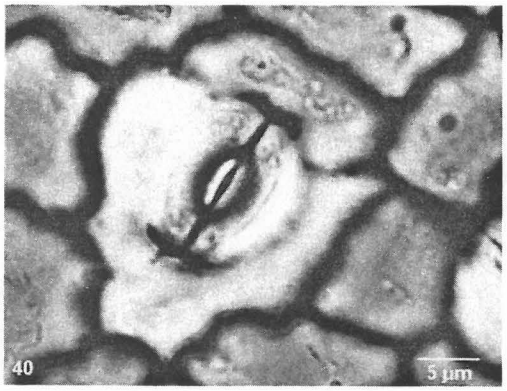


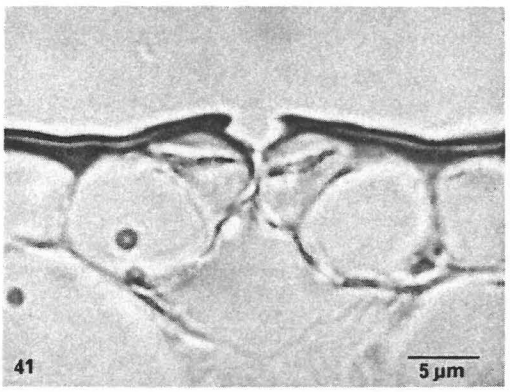












whether or not their shape and size are distinctive, is also recognized by Metcalfe & Chalk (1979).

According to the definition of Metcalfe & Chalk (1979), all of the southern African species of *Eugenia* have true subsidiary cells which differ from the surrounding cells mainly by their higher tanniniferous contents, lipid bodies and thicker cuticular membranes. The subsidiary cells of *E. uniflora* are tanniniferous and show a definite pattern of arrangement, whilst these cells are absent in *E. incerta*.

Whether the lipid bodies represent oil droplets or elaioplasts (Clowes & Juniper, 1968), still needs to be clarified. However, the possibility that they are spherosomes (often associated with stomata) can be ruled out on account of their larger size, small numbers per cell and staining reaction with the three Sudan stains (Sorokin & Sorokin, 1966). Using Sudan Black B, Patel *et al.* (1975) found that the subsidiary cells of the fern, *Athromeris wallichiana* (Spr.) Ching, can be distinguished clearly from epidermal cells and guard cells by the absence of lipid bodies. By using the same stain on some members of the Zingiberaceae, Raju & Shah (1975) reported that in mature healthy leaves lipid bodies are restricted to the subsidiary cells.

Ontogenetic classifications of stomatal types can, in spite of their desirability, be rather confusing because various systems have been proposed (Pant, 1965; Fryns-Claessens & Van Cotthem, 1973; Stevens & Martin, 1978; Payne, 1979). A general classification based upon mature topography is still more desirable for descriptive purposes. A system, based on the shape and arrangement of the subsidiary cells was originally proposed by Metcalfe & Chalk (1950). This classification has been greatly expanded by the discovery and description of several new stomatal types which has from time to time been reviewed, defined and often redefined by Stace (1965), Payne (1970), Van Cotthem (1970, 1971), Dilcher (1974), Brett (1979) and Metcalfe & Chalk (1979).

In a topographical classification, stomata of *E. uniflora* are identified as paracytic (thereby confirming the results of Ferri, 1971) and those of *E. incerta* are anomocytic. The water-stomata of the southern African species of *Eugenia* are often actinocytic (Fig. 12), a common feature in other groups of plants (Metcalfe & Chalk, 1979).

However, the regular stomata of the southern African species do not fit neatly into any of the hitherto proposed categories. Although at least some of the stomata of the indigenous species can be classified as staurocytic and others as anomotetracyctic, it seems better to retain the two categories proposed for stomata predominantly surrounded by four (sometimes three or five) similar subsidiary cells arranged in the patterns described by Van Cotthem (1970, 1971), Fryns-Claessens & Van Cotthem (1973) and Dilcher (1974). If the pre-requisite for four subsidiary cells in the definition for staurocytic stomata could include numbers varying from three to five (Metcalfe & Chalk, 1979), we would suggest

Figures 34–41. Stomatal morphology of *Eugenia uniflora* and *E. incerta*. Fig. 34. *E. uniflora*, stoma and part of water-stoma upper right. Fig. 35. *E. uniflora*, paracytic stomata. Fig. 36. *E. uniflora*, stomata with two, three and four subsidiary cells, respectively. Fig. 37. *E. uniflora*, epidermis stained with Sudan Black B showing the absence of lipid bodies (all from *Van Wyk, 1310*). Fig. 38. *E. incerta*, stoma. Fig. 39. *E. incerta*, epidermis stained with Sudan Black B showing the absence of subsidiary cells and lipid bodies. Fig. 40. *E. incerta*, stoma showing polar T-pieces. Fig. 41. *E. incerta*, transverse section of stoma stained with Sudan Black B to show the position of the cuticular membrane (all from *Van Wyk, 1259*). Scale for Figs 34 & 38: 1 segment of scale line = 10 μm.

anomostaurocytic as a more appropriate term for the stomatal type of the southern African species of *Eugenia*. The anomotetracytic type (Dilcher, 1974), which as the name implies, refers to stomata with four subsidiary cells, is not appropriate since 3–5 subsidiary cells occur. If the cell contents (which can not be demonstrated in cuticular preparations) and variation in cuticular membrane thickness of the epidermal cells are ignored, these stomata could be classified as anomocytic. Thus, it would seem that the anomostaurocytic stomatal type is probably only a modification of the anomocytic type. However, we still regard the additional term anomostaurocytic stomata necessary to provide a category for the southern African species of *Eugenia*.

Taxonomic value of stomata

Our observations indicate that the stomatal morphologies of the southern African species of *Eugenia* are not closely related to *E. uniflora* and *E. incerta*. Furthermore, the occurrence of anomocytic stomata and polar T-pieces in *E. incerta* and the absence of some in indigenous species, support the view already expressed by Dümmer (1912) that this species might not be indigenous to southern Africa.

Van Wyk *et al.* (1980) proposed a subdivision of the southern African species of *Eugenia*, based on periderm morphology, into two *ad hoc* groups X and Y. More evidence for this subdivision was supplied by Van Wyk (1980), with his paper on seed morphology. In this investigation, it was further found that a 100% correlation exists between stomatal, seed and periderm morphology. It is for this reason that in the text we referred to stomatal type X and Y. The alternative delimitation of some of the southern African taxa proposed by White (1977, 1978) and adopted by Coates Palgrave (1977) differs from that of Van Wyk *et al.* (1980). Evidence on stomatal morphology derived from this investigation supports the latter view.

However, the differences between groups X and Y must not be over-emphasized, since characters such as the presence of lipid bodies in the subsidiary cells and the more or less similar shape and arrangement of these cells occur commonly throughout southern African species.

The taxonomic value of variation in stomatal ledge width between species is probably limited as it shows an almost 100% correlation (0.869) with the thickness of the adaxial cuticular membrane (Van Wyk, 1978).

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APPENDIX

Voucher specimens. Unless otherwise stated, all collection numbers are those of Van Wyk. The specimens are deposited in the H. G. W. J. Schweickerdt Herbarium (PRU).

Eugenia albanensis Sonder: *1250; 1342; 1610; 1613; 1690; Ward 4530* (PRE).*
E. capensis (Ecklon & Zeyher) Sonder: *A38;* 987; 1262; 1308;* 1543; 1544; 1637; 2619; 4226;* Edwards 1737* (PRE); Strey 7139* (PRE).*
E. erythrophylla Strey: *1275; 1348; 1369; 1548; 1583; 1698; Jenkins s.n.* (PRE).*
E. incerta Dümmer: *1259.*
E. cf. *mossambicensis* Engl.: *971; 1149; 1299; 2495; Cooper 36* (PRE); Kruger 305* (PRE); v/d Schijff 3751* (PRE).*
E. natalitia Sonder: *950; 951; 1252; 1372; 1541; 1701; Botha 1525 (PUC); Moll 3327* (PRE); Ward 3327* (PRE).*
E. pusilla N.E. Br.: ***Forbes s.n. sub PRE 6350 (PRE).***
E. simii Dümmer: *A56;* 1269; 1664; 1680; 2148.*
E. uniflora L.: *1310.*
E. verdoorniae Van Wyk: *1616; 1617; 1622; 1681; 1696; 1700; 4225.*
E. woodii Dümmer: *825; 826; 905; 1122; 4227.**
E. zeyheri Harvey: *1291; 1296; 2131.*
E. zuluensis Dümmer: *1010; 1241; 1242; 1244; 1248;* 2153.**

*No measurements made of stomata.

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CHAPTER 3

TAXOMETRICS OF FOLIAR ORGANOGRAPHY

The genus *Eugenia* (Myrtaceae) in southern Africa: Taxometrics of foliar organography

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Six southern African species of the genus *Eugenia* L. were compared by means of a numerical analysis applying 20 mainly quantitative foliar organographic properties to determine the taxonomic value of these properties.

Leaves were cleared, stained and permanently mounted. Properties were measured on photographs obtained from mounts by using these directly as negatives. Two computer programs for cluster analysis and one for principal component analysis were employed.

The results conform to the delimitation of the species as currently recognized and show that foliar organography can be of taxonomic value.

S. Afr. J. Bot. 1982, 1: 147 – 157

Ses suider-Afrikaanse spesies van die genus *Eugenia* L. is met behulp van 'n numeriese analise waarin 20 hoofsaaklik kwantitatiewe blaar-organografiese kenmerke gebruik is, met mekaar vergelyk om die taksonomiese waarde van hierdie kenmerke te bepaal.

Blare is verhelder, gekleur en permanent gemonteer. Kenmerkwaardes is bepaal vanaf foto's wat verkry is deur die preparate direk as negatiewe te gebruik. Die waardes is met twee rekenaarprogramme vir groeperingsanalise en een vir hoofkomponent-analise verwerk.

Die resultate stem in die meeste gevalle ooreen met die huidige omgrensing van die spesies en dui op die bruikbaarheid van loofblaar-organografiese kenmerke in plant-taksonomie.

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Keywords: *Eugenia*, foliar organography, Myrtaceae, taxometrics, venation.

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1. Introduction

Foliage leaves of southern African species of *Eugenia* are rather similar in being simple and entire, usually opposite (rarely sub-opposite or ternate), brochidodromous and glandular-punctate. Nevertheless a limited number of foliar properties are frequently used for the delimitation of taxa. In this regard leaf shape and venation properties are most frequently employed.

Foliar properties proposed by Hickey (1973), Dilcher (1974), Mädler (1975) and Weber (1978) are mainly qualitative and suitable for descriptive rather than taxometric purposes. Hill (1980) introduced several quantitative foliar properties and successfully applied these to a numerical analysis of leaves of 20 randomly chosen species.

The purpose of the present study was

(a) to develop a clearing, staining and permanent mounting technique for leaves of indigenous species of *Eugenia*,
(b) to compare leaves of six species of *Eugenia* by means of a numerical analysis demonstrating the use of Hill's (1980) method and implementing as many quantitative properties as possible, and
(c) to ascertain whether the results of numerical analysis conform to the current delimitation of taxa which is usually based on a limited number of properties.

In view of the limited time that was available for this study and the laborious task involved in determining mainly quantitative properties, only a limited number of properties and individuals was employed. It is, however, possible to increase these substantially. Therefore the present study may be regarded as preliminary to a study with more extensive sampling and a wider range of properties.

2. Material and Methods

2.1 Material

The southern African species of *Eugenia* are divided into two groups, X and Y, on the basis of periderm (Van Wyk *et al.* 1980), seed (Van Wyk 1980), stomatal (Van Wyk *et al.* 1982) and other anatomical characters (Van Wyk 1978). FAA-fixed leaves of three species of each group were studied (Table 1).

With regard to each property each individual is represented by the average figure obtained from five leaves. In view of the rather invariant leaves of the southern African *Eugenia* species, the four to seven individuals

Table 1 Species of *Eugenia* and number of leaves studied

Group	Species	Number of individuals	Number of leaves/ individual	Total number of leaves/ species
X	*E. capensis* (Eckl. & Zeyh.) Sond.	5	5	25
X	*E.* cf. *mossambicensis* Engl.	5	5	25
X	*E. simii* Dümmer	4	5	20
Y	*E. albanensis* Sond.	7	5	35
Y	*E. verdoorniae* Van Wyk	5	5	25
Y	*E. zuluensis* Dümmer	5	5	25
Total		31	5	155

representing a species are regarded as adequate sampling for the present study. Voucher specimens are listed in the Appendix.

2.2 Methods

(a) *Clearing*

Clearing is based on the method of O'Brien and Von Teichman (1974) for 'difficult' specimens. The use of the autoclave (250 kPa at 125 °C for approximately 15 min) in this method speeds up the process, making it possible to clear a leaf within one day.

Bleached leaves are rinsed in water and left overnight in Stockwell's solution (Johansen 1940). Afterwards the leaves are again thoroughly rinsed in water.

(b) *Staining*

Cleared leaves may either be placed in 50% ethanol for five minutes and stained overnight in a safranin O solution (Johansen 1940) or, following Blackburn (1978), stained in a 0,1 mol dm^{-3} potassium permanganate solution for approximately five min.

Excess safranin O is removed from the material with two or three changes of 50% ethanol. Leaves stained with potassium permanganate are thoroughly rinsed in water.

(c) *Mounting*

Cleared leaves are dehydrated with acetone and infiltrated with 'Jackson's 1935 Polyester Resin' according to the following schedule (the ratios indicated refer to volume and indications of time are only approximate): Leaves are transferred to a mixture of two parts water, one part ethanol and one part acetone for 15 min. The material is then transferred to a mixture of one part water and one part acetone for 15 min, then to a mixture of one part water and four parts acetone for 15 min and then to a mixture of one part water and nine parts acetone also for 15 min. The material is then placed in acetone and after 15 min the acetone is replaced with fresh acetone in which it stays for 15 min. The leaves are then transferred to a mixture of one part acetone and one part polyester resin for 30 min and finally to polyester resin for 20 min.

The mounting medium is prepared by mixing the polyester resin and the catalyst supplied with it in a 50 : 1 mass ratio. Each leaf is mounted between two glass slides. No weights should be placed on drying mounts.

(d) *Photographic prints*

Mounted leaves were placed directly in the negative carrier of a photographic enlarger and printed on photographic paper (200 mm × 260 mm). All properties except No.'s 1, 2, 18, 19 and 20 (see below) were determined from these photographs.

(e) *Properties*

Fifteen quantitative properties proposed by Hill (1980) (No.'s 1 – 4 and 6 – 16), three newly defined quantitative properties (No.'s 5, 17 and 18) and two binary properties used by Van Wyk (1978) (No.'s 19 and 20) were employed (Table 2).

Table 2 List of properties

Number	Property	Unit
1	Leaf length	mm
2	Leaf width	mm
3	Leaf length/leaf width	–
4	Position of maximum leaf width	%
5	Primary vein length percentage	%
6	Leaf shape index	–
7	Leaf base angle	degrees
8	Leaf apex angle	degrees
9	Position of 20% maximum width basally	%
10	Position of 20% maximum width apically	%
11	Number of secondary veins	–
12	Intersecondary vein percentage	%
13	Secondary vein intercostal shape	–
14	Basal secondary vein angle	degrees
15	Secondary vein angle a	degrees
16	Secondary vein angle b	degrees
17	Marginal vein index	–
18	Areole number	–
19	Stomatal Type: 19.1 Type X	–
	19.2 Type Y	–
20	Appearance of primary vein adaxially:	
	20.1 Conspicuously raised primary vein present	–
	20.2 Conspicuously raised primary vein absent	–

All vein lengths, i.e. those of the primary (property 5) and the laterals (property 11) were measured (following vein curvature) with a MOP-AMO 3 Kontron Image Analyzer.

Property 1, leaf length (Hill 1980), was slightly modified to allow for the blade of *E. capensis*, the basal part of which often extends beyond the point of insertion of the petiole. The primary vein was extrapolated basally to the point where it met the tangent to the margins of the two basal leaf blade parts. Leaf length of *E. capensis* was measured from this point to the leaf apex (Figure 1).

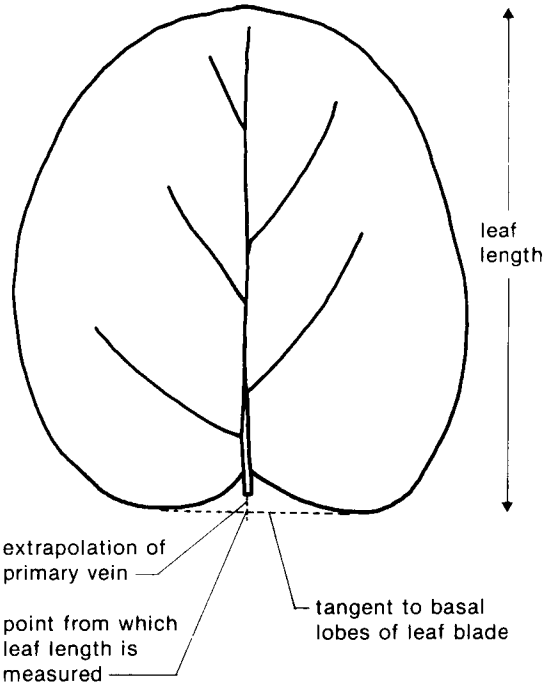


Figure 1 Determination of leaf length (property 1) in *Eugenia capensis*.

Property 5 is calculated as follows:

$$\text{Primary vein length percentage} = \frac{\text{Primary vein length}}{\text{leaf length}} \times 100$$

Primary vein length is measured from the point of insertion of the petiole to the end of the primary vein. Hill (1980) defines the end of a primary vein as the point at which it gives rise to a lateral vein of equal thickness to the continuation of the primary vein.

Property 17, marginal vein index, is determined as follows: from the end of every secondary vein terminating at the marginal vein, the perpendicular distance to the leaf margin is measured (Figure 2). The mean value, m, per leaf is used in the following formula:

$$\text{Leaf margin index} = \frac{m}{\text{leaf width}} \times 200$$

Property 18, areole number is determined directly from the mount with a stereo microscope. At the position of maximum leaf width the number of areoles along 10 mm and adjacent to the marginal side of the marginal vein is counted. This area is chosen in such a way that the position of maximum leaf width is in the centre of the 10 mm distance (Figure 3). The count is made on both the right and left sides of a mount, the mean of the two values being given as the areole number. For the sake of convenience a counting area was always positioned from left to right in the field of vision. Areoles only partially included in the 10 mm counting range, are excluded from a count on the left-hand side and included on the right-hand side of the counting range.

Property 19, stomatal type (Van Wyk *et al.* 1982), was determined on dried leaves from voucher specimens. Leaves were prepared according to standard methods and viewed with a scanning electron microscope (Figure 4).

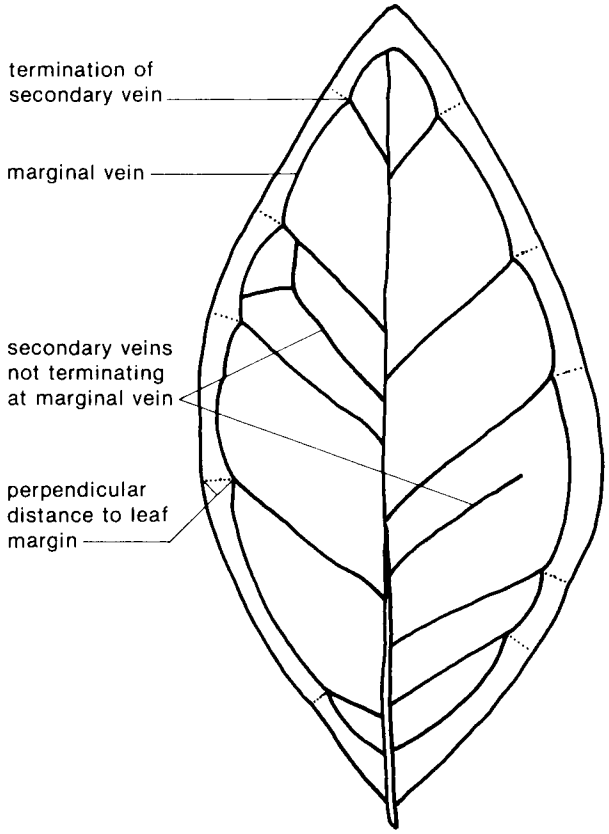


Figure 2 Determination of the marginal vein index (property 17).

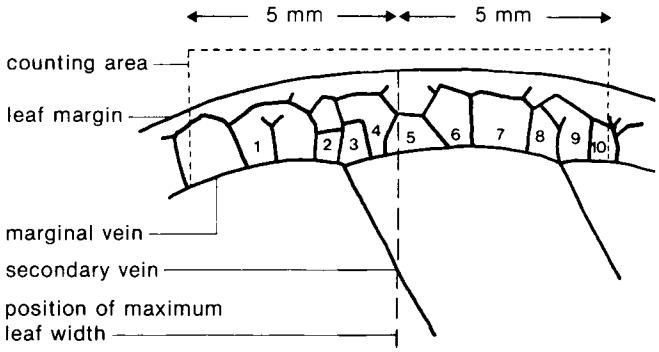
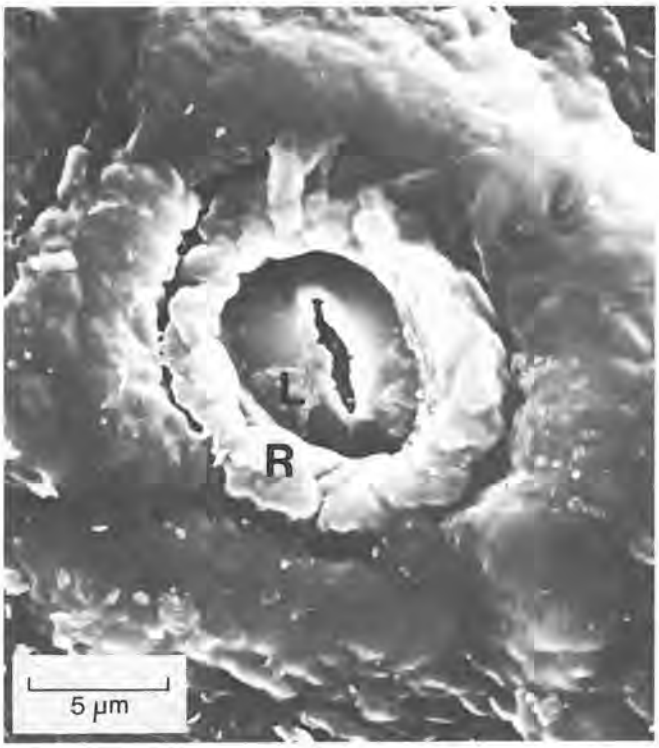


Figure 3 Determination of the areole number (property 18). Only secondary venation is shown on the primary vein side of the marginal vein. The figures indicate areoles counted on the right-hand side of the mount.

Property 20, appearance of the primary vein adaxially, indicates the presence or absence of a conspicuously raised primary vein and was determined on the adaxial leaf surface before leaf clearing (Figure 5). The occurrence of a midrib prominently raised adaxially is a rare property among southern African species of *Eugenia*. It is presently used (sometimes in combination with other properties) to separate *E. zuluensis* from all other indigenous species.

(f) *Standardization*

The mean of the values obtained from five leaves of an individual has been employed as the property value for each of the quantitative properties (No.'s 1 – 18). These property values were standardized using the method of Sturges (1926) as employed by Hill (1980).



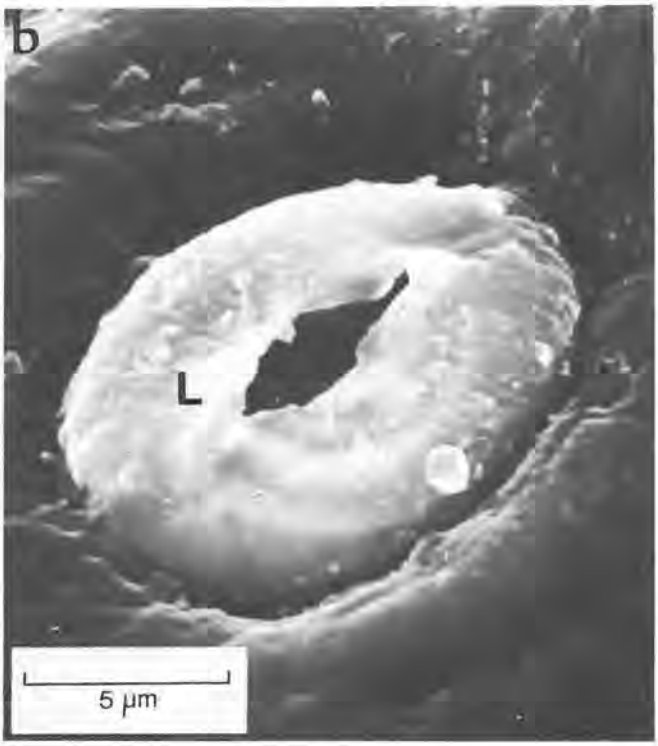


Figure 4 (a) Stomatal type X: *Eugenia simii*. Cuticular ledges (L) approximately horizontal with regard to blade surface and surrounded by a conspicuous cuticular ridge (R).
(b) Stomatal type Y: *Eugenia albanensis*. Cuticular ledges (L) dome-shaped with the alignment of the basal portion more or less perpendicular to the lamina surface and cuticular ridge absent.

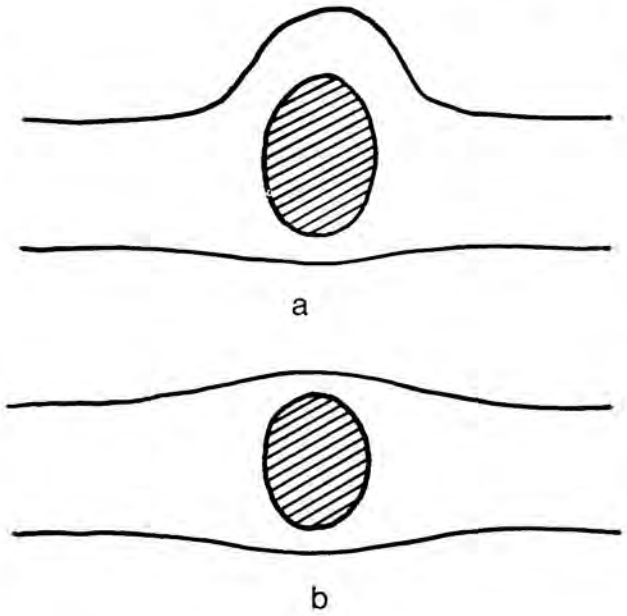


Figure 5 Schematic presentation of a transverse section of the primary vein region of a leaf blade illustrating the appearance of the primary vein adaxially (property 20). (a) Conspicuously raised primary vein present (b) Conspicuously raised primary vein absent.

(g) *Numerical analysis*

(i) *Cluster analysis*. Two computer programs for cluster analysis have been employed. The first has been written by Orloci and the methods employed are explained in Orloci (1967). It has been used among others by Lubke (1969) and Van der Westhuizen (1976). This program implements an agglomerative clustering method which operates on metric distance and uses the within-group sum of squares as the agglomeration criterion. Agglomeration is carried out in successive cycles in a manner such that the within-group sum of squares is minimized and, accordingly, the differences between the groups are maximized at each clustering cycles. In this way a hierarchy of dichotomous branching is constructed.

The second program has been developed by Steyn (Department of Statistics, P.U. for C.H.E., Potchefstroom) and Coetzee (Department of Botany, U.S., Stellenbosch) and used among others by Van Wyk (1978). The program calculates the percentage similarity (P_{ij}) between individuals and for purposes of this investigation the equation of Canberra (Coetzee, pers. comm.) was employed. The formula is:

$$P_{ij} = \left(1 - \frac{1}{n} \sum_{k=1}^{n} \frac{(X_{ik} - X_{jk})}{(X_{ik} + X_{jk})}\right) 100 \; ; \; i, j = 1, \ldots, N,$$

where X_{ik} is the value of property k of individual i, n is the number of properties and N is the number of individuals.

For qualitative properties the terms concerned in the summation become:

1 if $X_{ik} \neq X_{jk}$

0 if $X_{ik} = X_{jk}$

The percentage similarities are used to cluster the individuals by means of centroid linkage and a table from which a dendrogram can be constructed, is printed.

(ii) *Principal component analysis*. The principal components have been calculated by means of a computer program written by Morris (Datametrical Services, Department of Agriculture and Fisheries, Pretoria). See Ross & Morris (1971) for an explanation and application of the program.

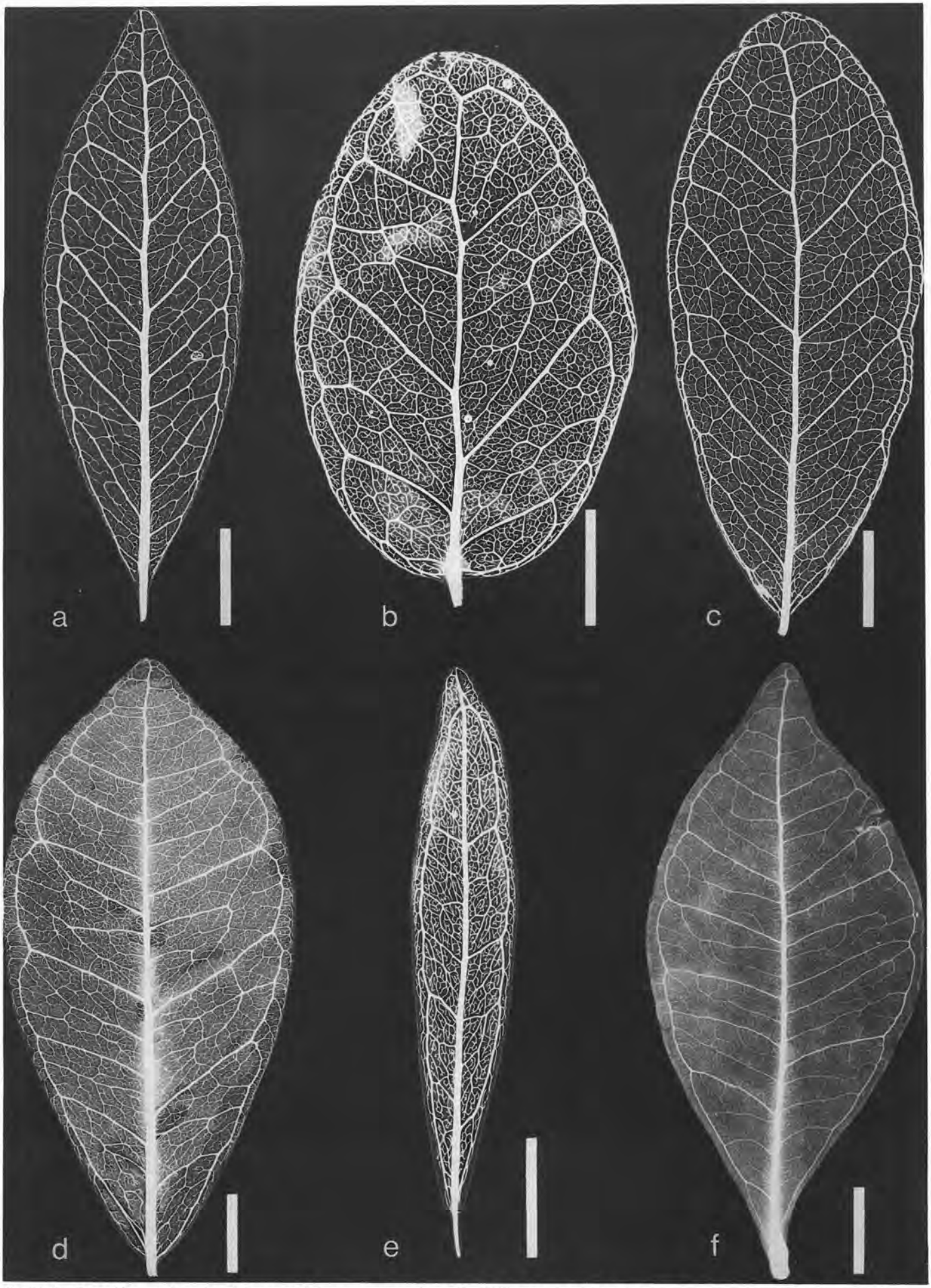


Figure 6 Cleared leaves of species of *Eugenia* (a) *E. simii*, stain: safranin O; (b) *E. capensis*, stain: potassium permanganate; (c) *E.* cf. *mossambicensis*, stain: safranin O; (d) *E. albanensis*, stain: safranin O; (e) *E. verdoorniae*, stain: potassium permanganate; (f) *E. zuluensis*, stain: safranin O. Length of scale = 5 mm.

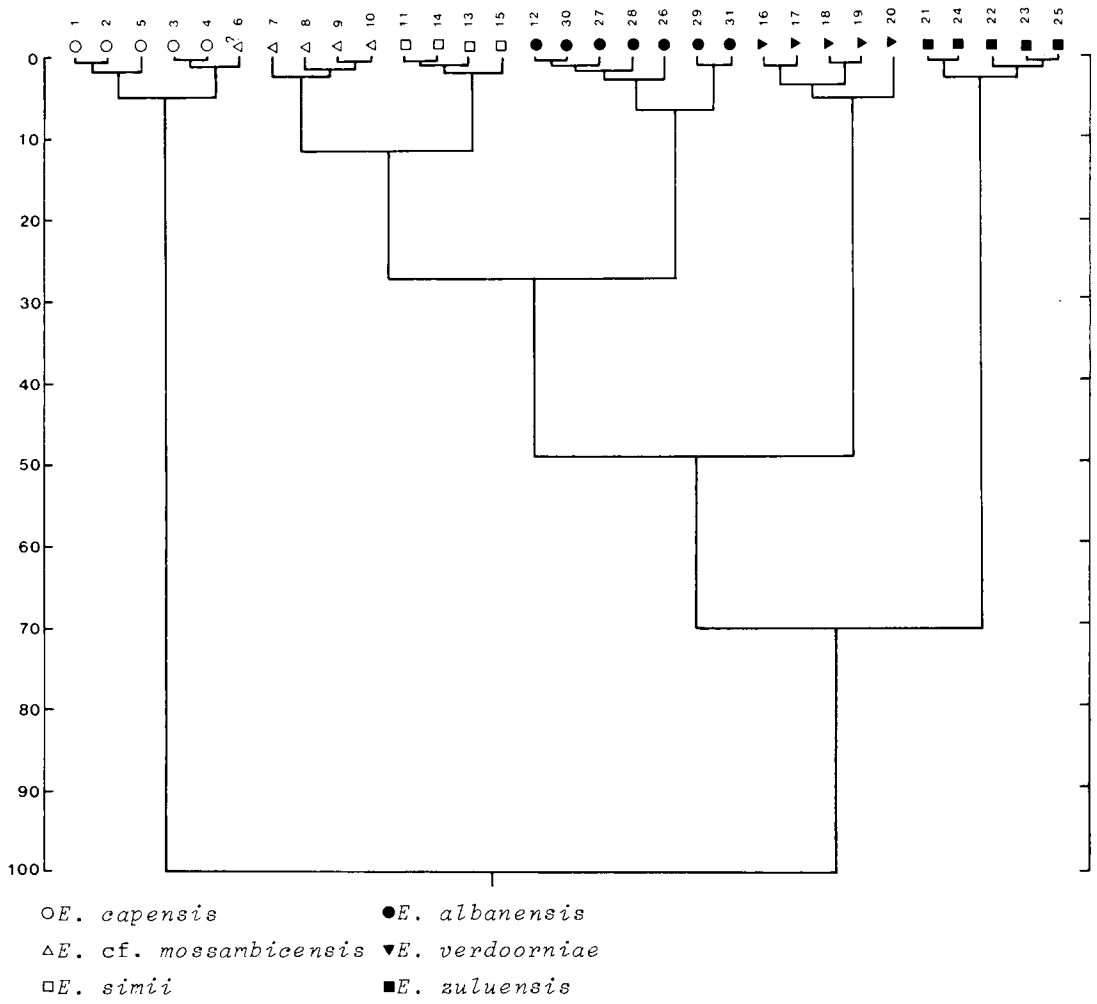


Figure 7 Phenogram for 31 individuals with 20 properties. Vertical scale indicates within-group mean squares expressed as percentages of the sample mean square. Computer program: Orloci (1967).

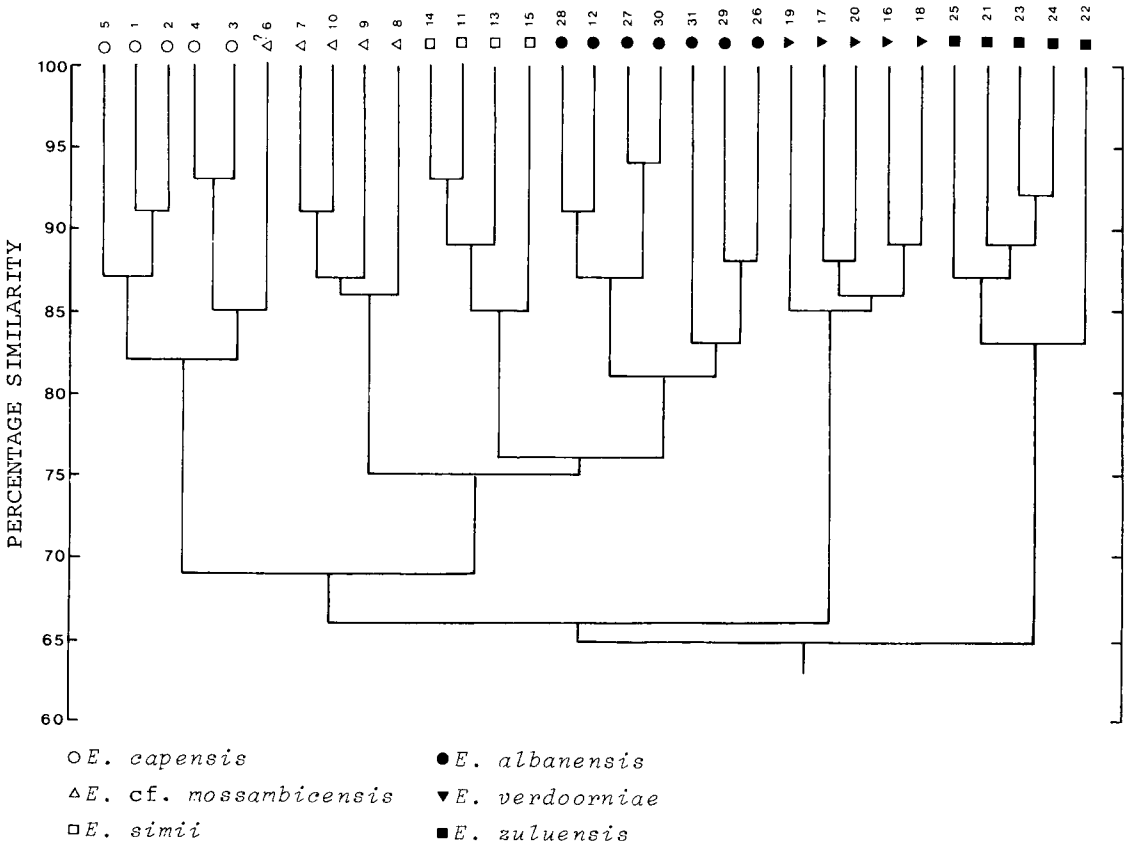


Figure 8 Phenogram for 31 individuals with 20 properties. Computer program: Steyn & Coetzee.

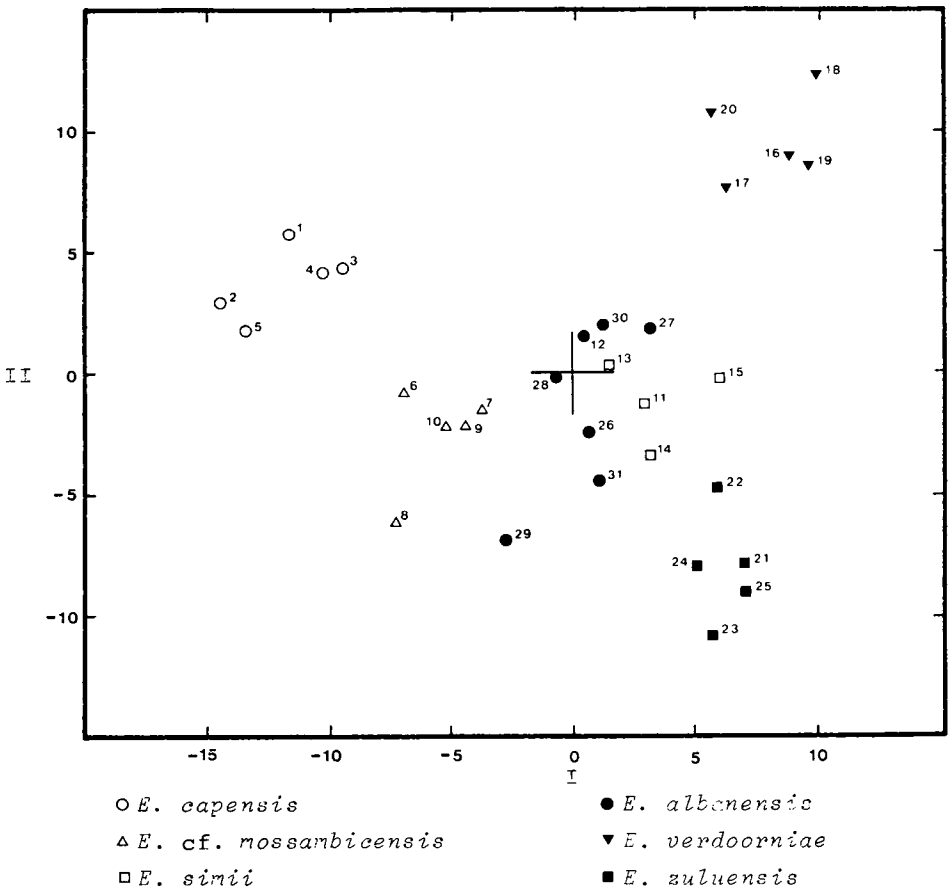


Figure 9 Ordination diagram of the first two components of a principal component analysis on 31 individuals with 20 properties. Variance accounted for: component I — 31,5%; component II — 25,2%.

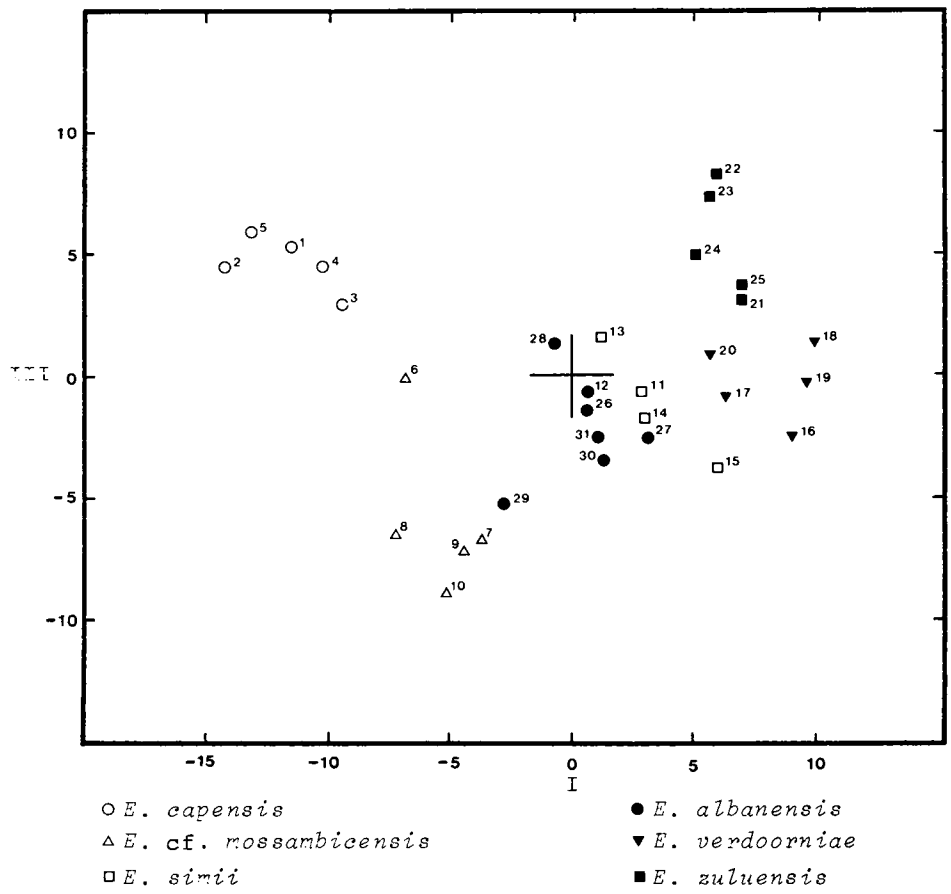


Figure 10 Ordination diagram of the first and third components of a principal component analysis on 31 individuals with 20 properties. Variance accounted for: component I — 31,5%, component III — 15,3%.

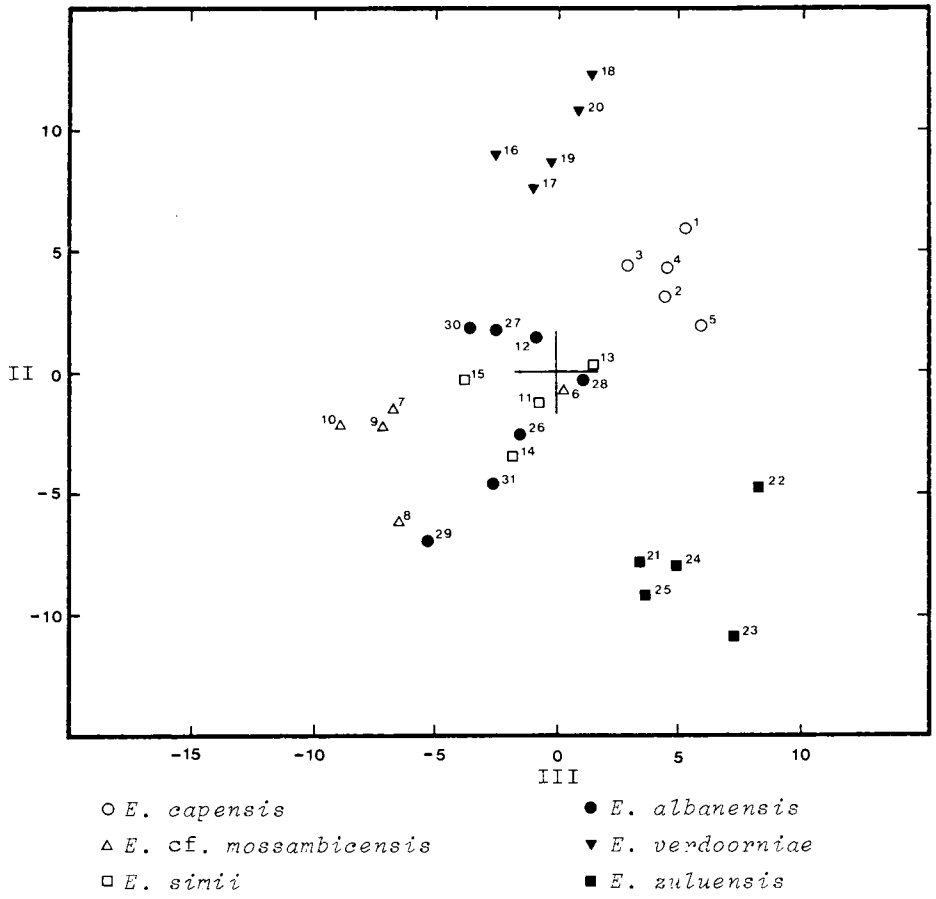


Figure 11 Ordination diagram of the second and third components of a principal component analysis on 31 individuals with 20 properties. Variance accounted for: component II — 25,2%; component III — 15,3%.

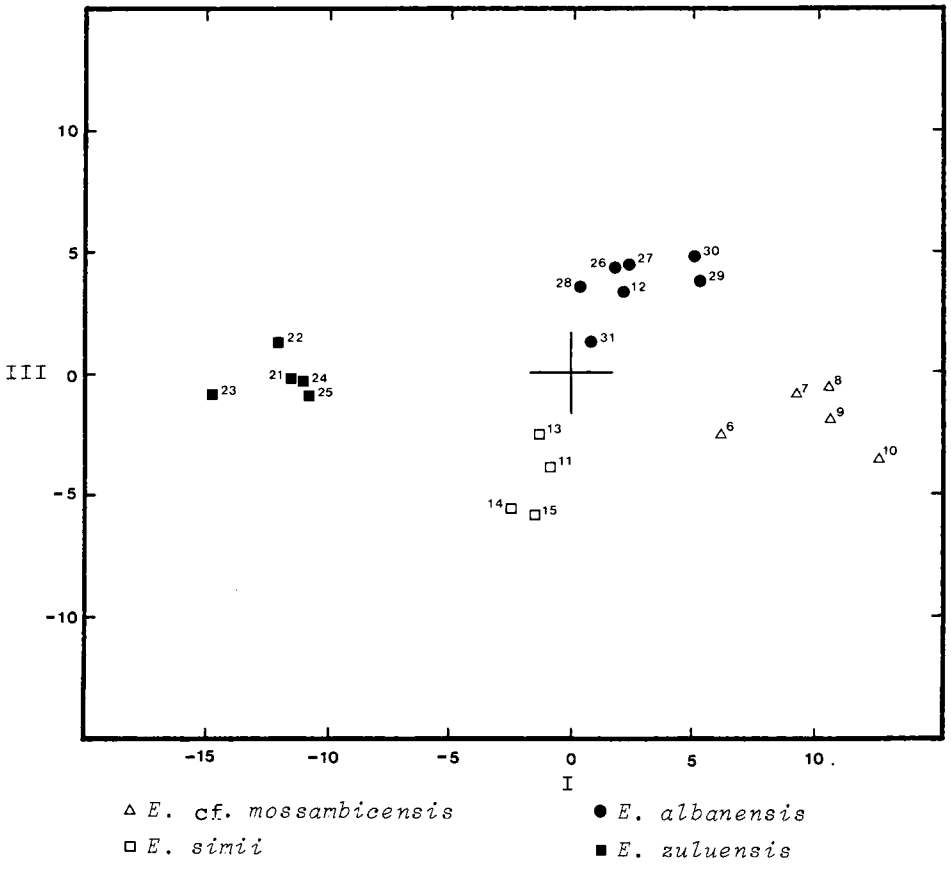


Figure 12 Ordination diagram of the first and third components of a principal component analysis on 21 individuals with 20 properties. Variance accounted for: component I — 34,8%; component III — 13,3%.

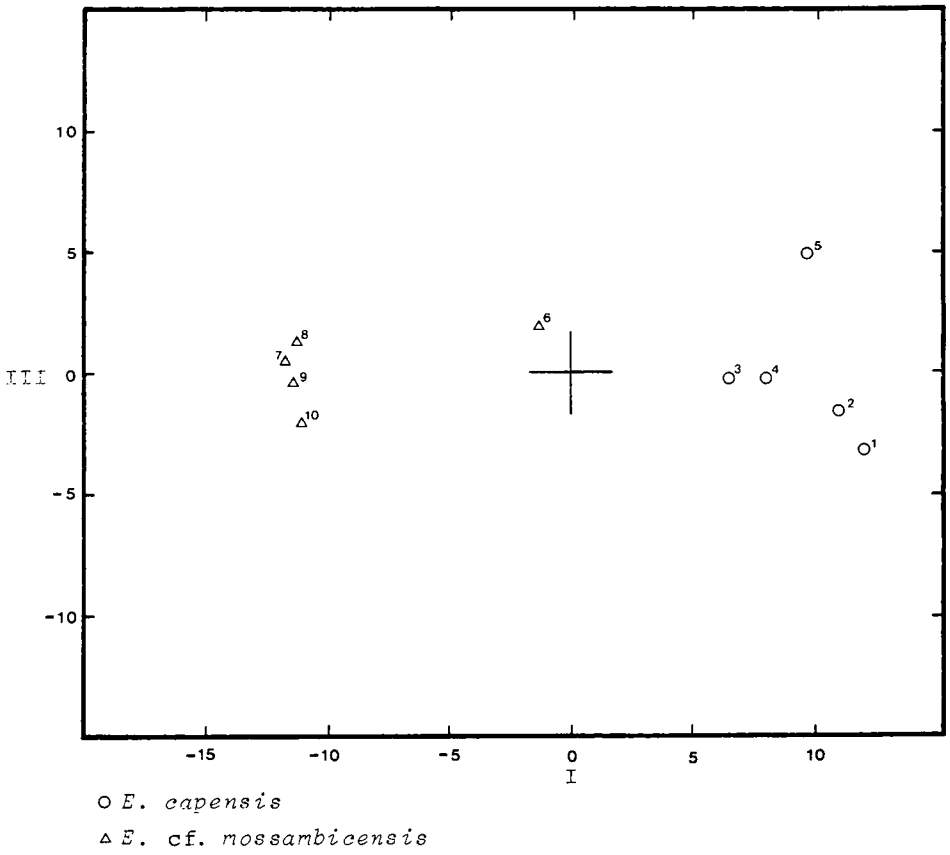


Figure 13 Ordination diagram of the first and third components of a principal component analysis on 10 individuals with 17 properties. Properties 3, 19 & 20 have been omitted. Variance accounted for: component I — 58,2%; component III — 10,0%.

3. Results

3.1 Permanent mounts and photographs

The clearing and mounting procedures were most effective and resulted in transparent permanent mounts.

Safranin O stained the veins from pink to dark red and gave a satisfactory contrast between veins and other leaf tissues. Potassium permanganate solution gave the best staining results. Within 5 min the veins stained dark brown, contrasting excellently with the surrounding leaf tissue.

Complete removal of the cuticular membrane (and sometimes epidermis) in specimens from group X proved to be possible following autoclaving. This resulted in improved contrast after staining.

Figure 6 shows prints of cleared, stained and permanently mounted leaves of each of the *Eugenia* spp. studied.

3.2 Numerical analysis

(a) *Cluster analysis*

The results are shown in Figures 7 & 8. With the exception of individual 6, the clustering of all individuals corresponds to the currently recognized species.

(b) *Principal component analysis*

The results are shown in Figures 9 – 13. Where standardized values were identical in all the individuals employed in a given principal component analysis, those properties were omitted.

4. Discussion

4.1 Permanent mounts

The use of the autoclave (O'Brien & Von Teichman 1974) with leaf clearing in KOH saves time. Christophel & Blackburn (1975) point out that a leaf of a *Cinnamomum* sp. has to be soaked in a KOH or NaOH solution for four weeks. Using the autoclave, the KOH stage lasted approximately 45 min for the *Eugenia* leaves in this investigation.

After autoclaving, the leaves in this study were soaked in household bleach for approximately 1 h. Leaves only soaked but not autoclaved in KOH, however, have to be bleached for two to seven days (Christophel & Blackburn 1975). Stockwell's solution (Johansen 1940) applied after bleaching, improved the staining results.

As for a stain, potassium permanganate is preferred to safranin O. According to Blackburn (1978) safranin O fades with time, the process appearing to be related to the presence of traces of catalyst in the mounting medium. In the case of potassium permanganate, an inorganic substance, the pigment itself is manganese dioxide, deposited from the reduction of the permanganate in the presence of lignin. This compound is chemically stable and should not fade with time.

The use of polyester resin (Christophel & Blackburn 1975) as mounting medium shortened the drying period considerably. Mountants such as Canada Balsam, Euparol and Permount, dry only after approximately three weeks. 'Jackson's 1935 Polyester Resin' used in this study dries within about 1 h. A further advantage is that the resin also aids in the clearing of the leaves.

The use of weights on the drying mounts is not recommended as this often causes the formation of opaque areas.

4.2 Numerical analysis

Phenograms based on both programs (Figures 7 & 8) cluster the individuals into the conventionally identified species, except individual 6 which groups with *E. capensis* instead of *E.* cf. *mossambicensis*.

The individuals of *E. capensis* group clearly in Figures 9, 10 & 11, and those of *E. verdoorniae* in Figures 9 & 11. In figure 12 the individuals of the remaining four species form distinct groups which correspond to current identification.

Individual 6, currently identified as *E.* cf. *mossambicensis* shows affinity to *E. capensis* (Figures 9, 10 & 11), the same trend having been indicated by the results of the cluster analysis. Presumably *E.* cf. *mossambicensis* represents a grassland form of *E. capensis*. Typical *E. capensis* occurs mostly as shrubs or trees on the coastal dunes of Natal and the eastern Cape where veld fires are relatively rare. *E.* cf. *mossambicensis*, usually with a dwarf shrub habit, occurs more inland e.g. in the grassland of Maputaland where it is regularly subjected to burning.

Individual 6 was collected in a rocky habitat in the eastern Transvaal where it apparently is rarely influenced by veld fires, while the other members of *E.* cf. *mossambicensis* included in this study grow in Maputaland and are often exposed to fire.

Since the flowers and fruits of *E. capensis* and *E.* cf. *mossambicensis* are almost identical, it is recommended that the possible relationship between the two taxa be investigated further by utilizing, among others, foliar properties.

The division of southern African species of *Eugenia* into groups X and Y (see 2.1) is reflected by neither the phenograms (Figures 7 & 8) nor by the ordination diagrams (Figures 9, 10 & 11). Nevertheless the structure of the stomata (property 19) as well as the easy removal of the cuticular membrane only in species from group X after autoclaving, support the proposed grouping.

This lack of concordance may be owing to the fact that a limited number of only leaf properties have been used. There also is the possibility of some inter-dependence among them. In fact, supporting evidence for the proposed grouping is also derived from stem, flower and seed morphology. Indeed results of a cluster analysis employing 73 anatomical leaf properties (Van Wyk 1978) show slightly more concordance with the proposed grouping than the results of the present study. If evaluated separately, six of these anatomical properties support it. Thus indications are that a limited number of properties for numerical analysis may tend to obscure supra-specific groupings. The same can be expected with a large number of properties of which many, if evaluated separately, are not supportive of such groupings.

The results illustrate the value of mainly quantitative foliar properties when only vegetative material is available such as in the case of fossils, even in taxa with relatively little leaf variation. These properties might also be useful in taxa showing little variation in flower and fruit properties, as in several *Eugenia* species. The results also support the usefulness of the quantitative foliar properties introduced by Hill (1980).

5. Conclusions

(a) Leaves of species of *Eugenia* were effectively cleared, stained, and permanently mounted, the mounts being directly usable for the production of enlarged photographic prints of the venation pattern of the leaves.

(b) The current delimitation of six species of *Eugenia* during which usually only a few properties are employed, is to a great extent supported by a combination of 18 quantitative and two qualitative foliar properties.

(c) The possible relationship between *E. capensis* and *E.* cf. *mossambicensis* deserves further study employing among other things, quantitative foliar organographic properties.

(d) Although Sneath and Sokal (1973) recommend a minimum number of 60 properties for a numerical study, clear grouping of individuals into clusters was obtained with only 20 properties.

(e) The determination of quantitative foliar properties is time consuming — the method is recommended only when very few or no other properties are available for study.

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Appendix List of voucher specimens. All specimen numbers are those of the second author. Specimens are deposited in PRU

Species	Grid reference	Specimen number	Individual number
Eugenia capensis	2832 CC Mtubatuba	994	1
,, ,,	2732 DA Ubombo	985	2
,, ,,	3327 CA Peddie	3166	3
,, ,,	3228 CB Butterworth	3245	4
,, ,,	3130 AA Port Edward	2618	5
Eugenia cf. *mossambicensis*	2531 CA Komatipoort	5521	6
,, ,,	2732 AC Ubombo	2495	7
,, ,,	2732 BC Ubombo	975	8
,, ,,	2732 BA Ubombo	979	9
,, ,,	2732 CA Ubombo	990	10
Eugenia simii	3030 CA Port Shepstone	1271	11
,, ,,	3030 CA Port Shepstone	1270	13
Eugenia simii	3130 AA Port Edward	1664	14
,, ,,	3030 CA Port Shepstone	3274	15
Eugenia verdoorniae	3030 CC Port Shepstone	3282	16
,, ,,	3030 CC Port Shepstone	1700	17
,, ,,	3030 CC Port Shepstone	2335	18
,, ,,	3129 BD Port St. Johns	1616	19
,, ,,	3129 BD Port St. Johns	1617	20
Eugenia zuluensis	2830 DB Dundee	1010	21
,, ,,	2930 AC Pietermaritzburg	1244	22
,, ,,	3029 DA Kokstad	3263	23
,, ,,	3029 DA Kokstad	3268	24
,, ,,	2930 AC Pietermaritzburg	1240	25
Eugenia albanensis	3130 AA Port Edward	1342	12
,, ,,	3129 BC Port St. Johns	1350	26
,, ,,	3326 BD Grahamstown	3209	27
,, ,,	3129 BD Port St. Johns	1552	28
,, ,,	3030 BD Port Shepstone	1264	29
,, ,,	3130 AA Port Edward	1690	30
,, ,,	2930 CB Pietermaritzburg	1247	31

CHAPTER 4

MORPHOLOGY, ONTOGENY AND TAXONOMIC VALUE OF THE SEED

Jl S. Afr. Bot. 46 (2): 115–119 (1980)

A NOTE ON THE SEED MORPHOLOGY OF THE GENUS *EUGENIA* L. (MYRTACEAE) IN SOUTHERN AFRICA

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ABSTRACT

The seed morphology of *Eugenia* L. in Southern Africa provides strong additional evidence in support of distinguishing between two species groups which were first recognised on the basis of anatomical characteristics. Descriptions are provided for each group of seeds.

These results could influence the taxonomic treatment of *Eugenia* L. occurring not only on the subcontinent, but throughout Africa.

UITTREKSEL

AANTEKENINGE OOR DIE SAADMORFOLOGIE VAN DIE GENUS *EUGENIA* L. (MYRTACEAE) IN SUIDER-AFRIKA

Die saadmorfologie van *Eugenia* L. in Suider-Afrika verskaf sterk, bykomende getuienis ter ondersteuning van 'n groepering van spesies in twee verskillende groepe wat aanvanklik op grond van anatomiese kenmerke voorgestel is. Beskrywings van die sade word vir elke groep verskaf.

Hierdie resultate kan die taksonomiese hersiening van *Eugenia* L. wat nie alleen in die sub-kontinent nie, maar ook in die res van Afrika voorkom, beïnvloed.

INTRODUCTION

A recent comparative anatomical investigation (Van Wyk, 1978; unpublished results) indicates that the *Eugenia* L. *sensu stricto* species of Southern Africa can be divided into two distinct groups based on certain anatomical characteristics (Van Wyk, Botha & Coetzee, 1980). Some of these characteristics enabled the author to distinguish between species which were confused in the past (Van Wyk, 1980). Consequently a critical study of the external morphology of the plants was undertaken in an attempt to find additional features which support the proposed grouping of the species.

In the present paper some preliminary results concerning the seed morphology are presented. The two species groups mentioned above will be referred to as Group X and Group Y.

In the taxonomy of the Myrtaceae, seed characteristics (especially embryonic structure) are of paramount importance in the delimitation of many genera and higher categories in the tribe Myrteae. The taxonomic value of the mature embryo was first recognised by De Candolle (1828) and today forms the basis of all the taxonomic treatments of this tribe (McVaugh, 1968).

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Despite the acknowledged taxonomic value of seed characteristics, it is often neglected in taxonomic work because of the lack of fruiting material in herbaria. The regional revisions of the genus *Eugenia* L. *sensu lato* for Malaya (Henderson, 1949) and Hawaii (Wilson, 1957) are probably two of the few works in which the nature of the seeds was described in some detail for many of the species.

Descriptions of the seeds of Southern African *Eugenia* species were mostly limited to vague comments pertaining to size, form and colour. In their revisions for Southern Africa, both Dümmer (1912) and White (1978) attached no obvious interspecific taxonomic significance to the seeds of this genus.

Material and Methods

Dried fruit from herbarium sheets was rehydrated by transferring to water and boiled for about 30 minutes. In rehydrated material, however, seed characteristics are not very reliable. If available, preference was thus given to fruits which were either fresh or preserved in formalin-acetic acid-alcohol (FAA).

All material was identified according to the criteria used in the original descriptions of the taxa and in most cases also by comparison with type specimens. The results are based on seeds from the following species:

GROUP X	GROUP Y
Eugenia capensis (Eckl. + Zeyh.) Sond.	*E. albanensis* Sond.
E. cf. *mossambicensis* Engl.	*E. erythrophylla* Strey
E. natalitia Sond.	*E. verdoorniae* Van Wyk
E. simii Dümmer	*E. woodii* Dümmer
	E. zeyheri Harv.
	E. zuluensis Dümmer

Results

Seeds of all the species possess a testa which is free from the pericarp and lies close to the surface of the embryo. The mature embryo consists of two apparently homogeneous, but in fact only partially fused, thick and fleshy plano-convex cotyledons, connected by a short radicular protuberance. A line of separation is visible on the more or less smooth surface of the embryo, between the cotyledons which lie side by side.

Apart from these mutual characteristics, species belonging to Group X differ in their seed structure from species belonging to Group Y. All the references to shape in the descriptions which follow, are based on seeds from fruits in which only one ovule had developed. If more than one ovule develops in the same fruit, the seeds are often variously compressed—this, however, is the exception rather than the rule.

GROUP X (Fig. 1): *Seed* (and embryo) reniform to subreniform, rarely oblong globose. *Testa* thin (c. 0,25 mm thick) and membranous, outer surface smooth,

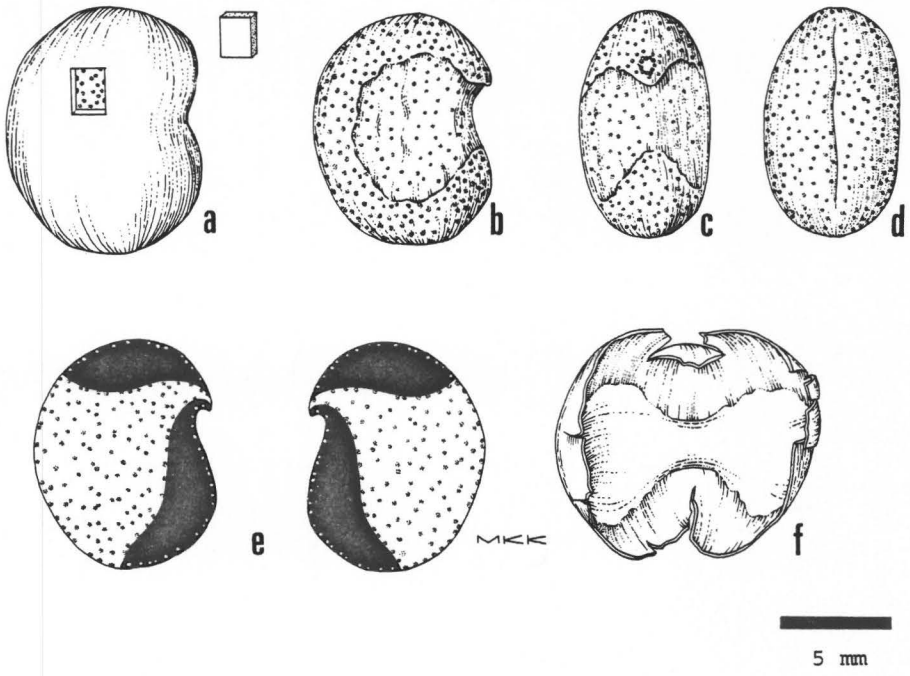

FIG. 1.
Seed morphology of *Eugenia natalitia* Sond.—GROUP X: a, seed with part of thin testa removed, showing surface of embryo beneath; b, lateral view of conspicuously glandular punctate embryo; c, ventral view of embryo showing spot of densely arranged glands on radicular protuberance; d, dorsal 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 slightly raised pattern on inner surface.

light brown; inner surface with a slightly raised, dark-coloured pattern resembling in outline two horseshoes connected between the open ends. *Cotyledons* equal, bright green (when fresh), all the free surfaces conspicuously glandular-punctate, opposing faces more or less plane; the line of demarcation more or less straight; outer surface of each cotyledon with a horseshoe-shaped pattern due to a slightly depressed or irregular cotyledon surface with often slightly smaller and lesser glands than the remaining surface: this pattern corresponds with the one on the testa. *Radicular protuberance* with a circular dark-coloured spot from which the radicle probably grows on germination.

GROUP Y (Fig. 2): *Seed* (and embryo) globose to subglobose. *Testa* thick (c. 1,0 mm) and woody, outer surface of one hemisphere more or less smooth and light brown, the other half thicker, covered by remains of the pericarp, dark coloured; inner surface with a prominent depression, lined with a whitish tissue. *Cotyledons* equal to nearly equal, pale green to greenish-white (when fresh),

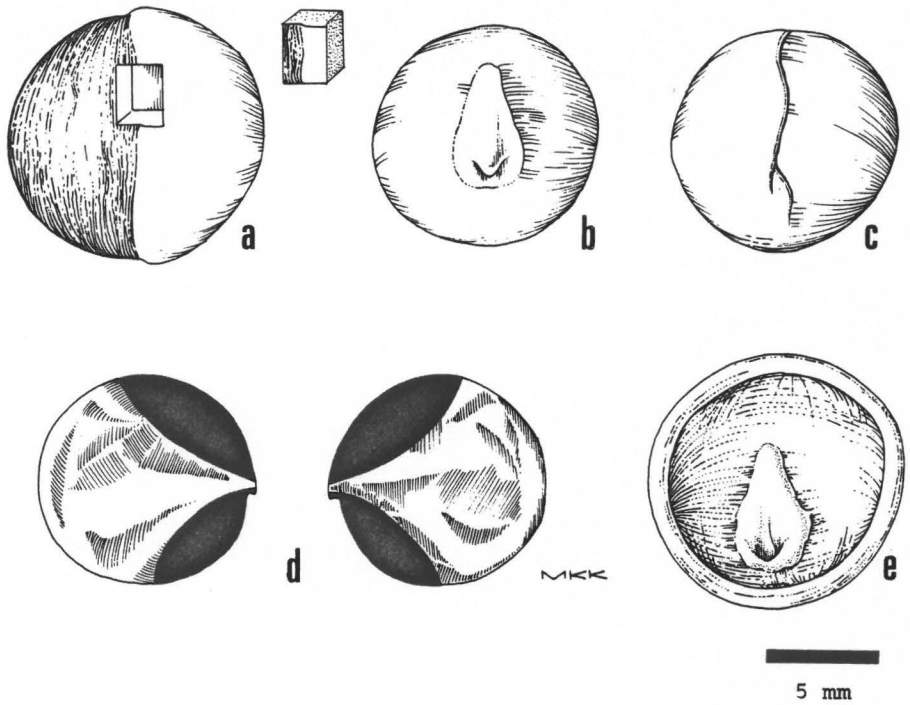

FIG. 2.
Seed morphology of *Eugenia zeyheri* Harv.—GROUP Y: a, seed with part of thick testa removed, showing embryo beneath; b, embryo with short radicular protuberance surrounded by a slightly raised light-coloured pattern; c, embryo with branched line of separation between the two cotyledons; d, split-open embryo, showing irregular inner surface of cotyledons and region of fusion (black); e, one half of testa, showing the light-coloured depressed pattern on inner surface.

apparently eglandular but usually with a few obscure glands mainly associated with the radicular protuberance; opposing faces usually somewhat concave or with ridges fitting into corresponding grooves, sometimes more or less plane; the line of demarcation straight, curved, or ramnified; outer surface of each cotyledon with a slightly raised, more or less linear, ovate or obovate, smooth-surfaced strip of tissue running around the radicular protuberance dorsally towards the start of the demarcation groove, fitting into the depression on the inner surface of the testa. *Radicular protuberance* with the spot from which the radicle grows (cf. Group X) probably present, but obscure.

DISCUSSION

The division of the Southern African *Eugenia* species into two groups on the basis of anatomical characteristics is correlated with two morphologically different

kinds of seed. This points towards the existence of at least two major lines of evolution in the local members of this genus.

It would appear that the species of Group X and Group Y are in fact not as closely related as was believed by previous authors. According to the present results the delimitation of some of the taxa proposed by White (1977, 1978) needs serious reconsideration.

Amshoff (1958) believed that the African members of *Eugenia* have the testa probably adhering to the pericarp, thus differing from the American members, in which the testa is free. This, however, was not confirmed by the present study. In all the species examined the testa remains on the cotyledons when the pericarp is removed. Furthermore, the seeds of Group X closely resemble those of *E. uniflora* L. from South America, which is the lectotype species for the genus *Eugenia* L.

For the present, no suggestions are made as to a formal taxonomic rank for Group X and Group Y. Features of much more African species need to be studied to ascertain the full taxonomic implications of these findings.

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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.

S. Afr. J. Bot. 1984, 3: 63 – 80

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.

S.-Afr. Tydskr. Plantk. 1984, 3: 63 – 80

Keywords: Anatomy, *Eugenia*, Myrtaceae, ontogeny, seed, taxonomy

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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.

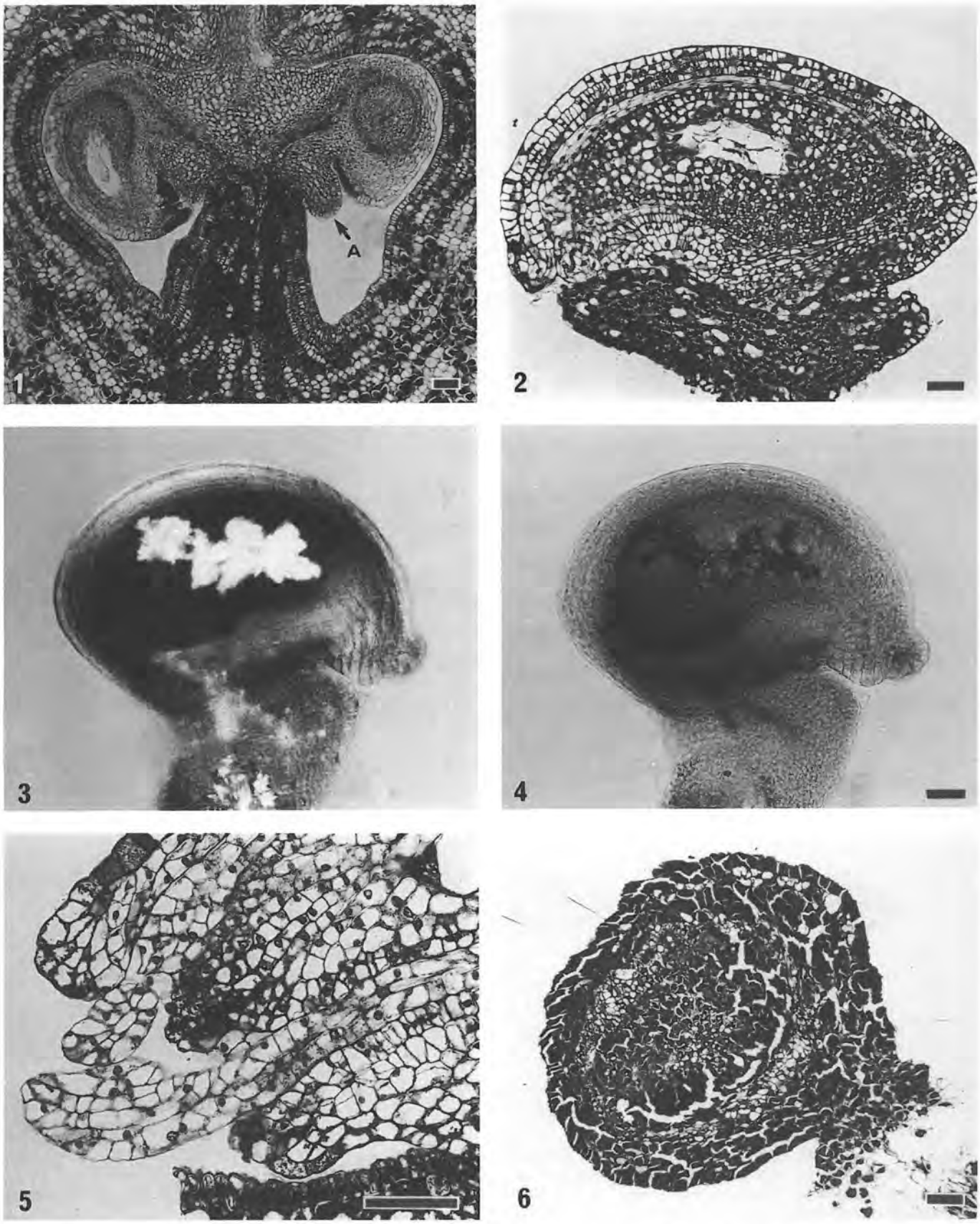
Usually only one (rarely two to three) ovule per ovary matures into a seed. The abortive ovules are transformed into ovulodes (see 3.4). Our observations indicate that the salient features of seed development are similar in all the species of a single group. This supports our initial assumption. Despite 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.

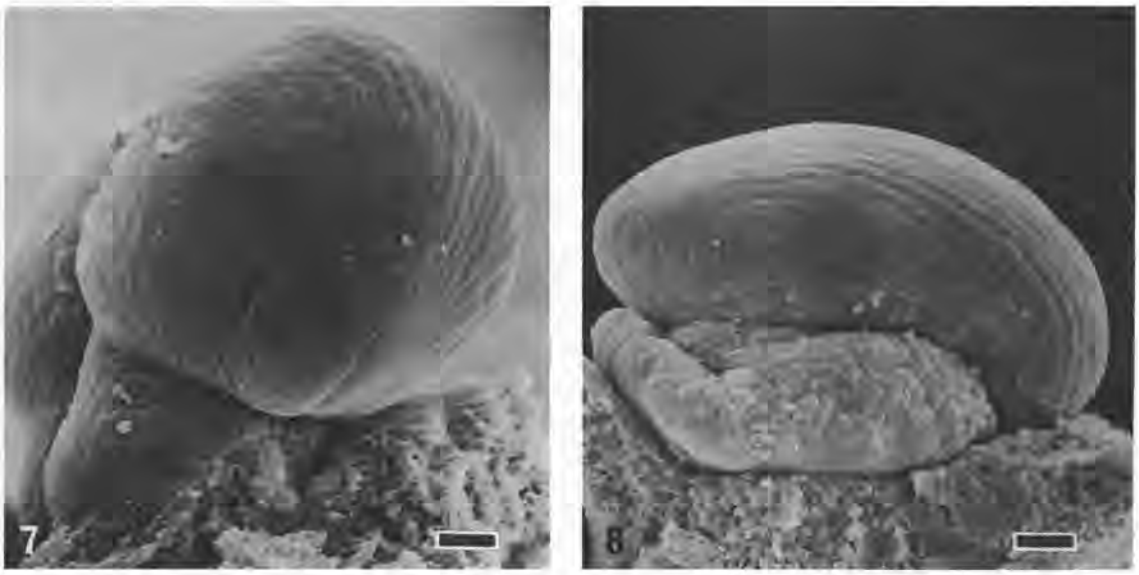
The relatively thin, leathery or rather brittle (when dried out) testa develops from the outer integument. At an early stage of development the inner integument is crushed although vestiges of its thicker distal part persist somewhat longer in the micropylar region (Figures 11B & 15). Limited divisions 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.

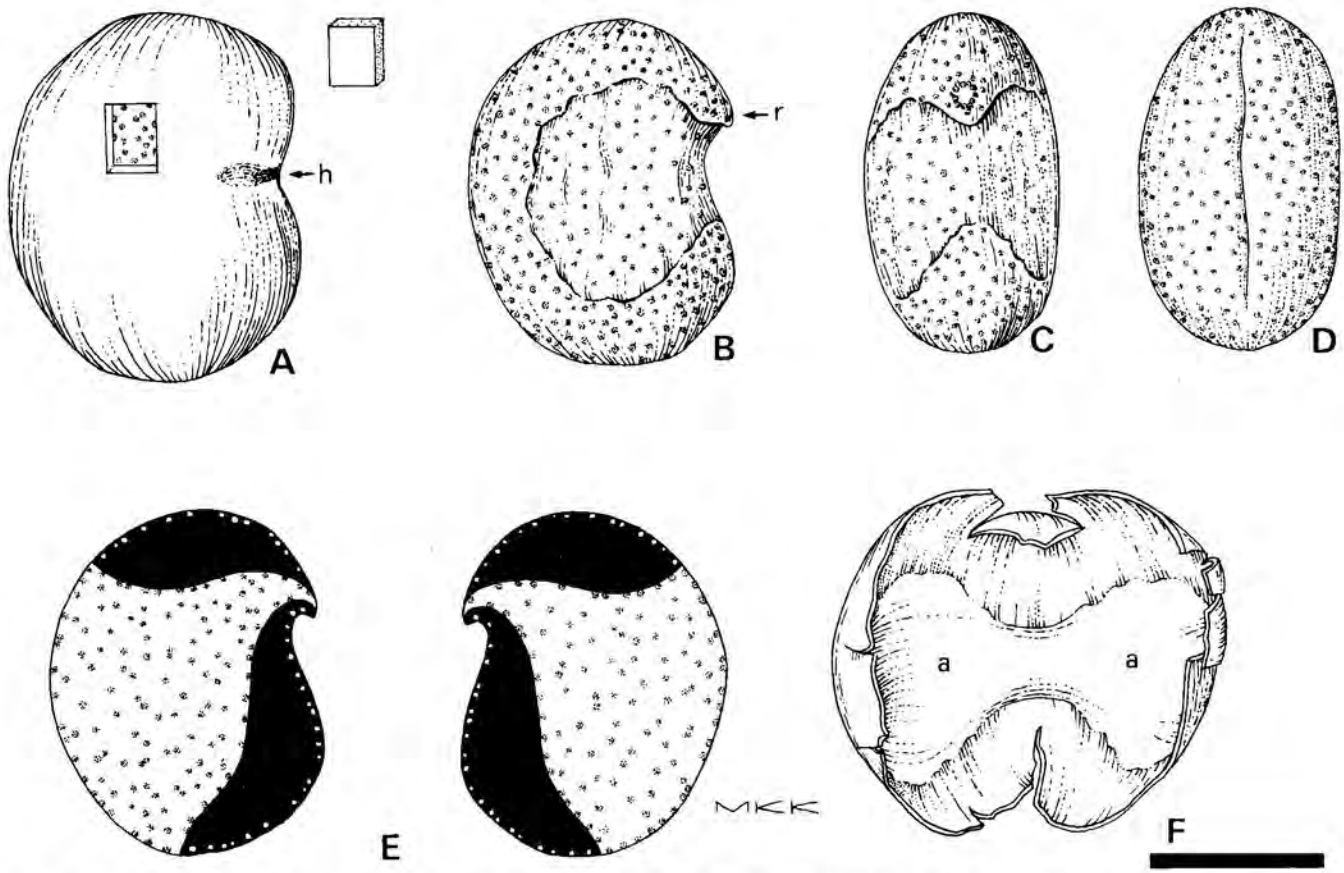


Figure 9A – F Morphology of seed type X. Mature seed of *E. natalitia* (*Van Wyk* 4854). A. Seed with part of testa removed showing surface of embryo beneath. B. Lateral view of glandular punctate embryo showing the impression left by the areolae. C. Ventral view of embryo showing spot of densely arranged 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

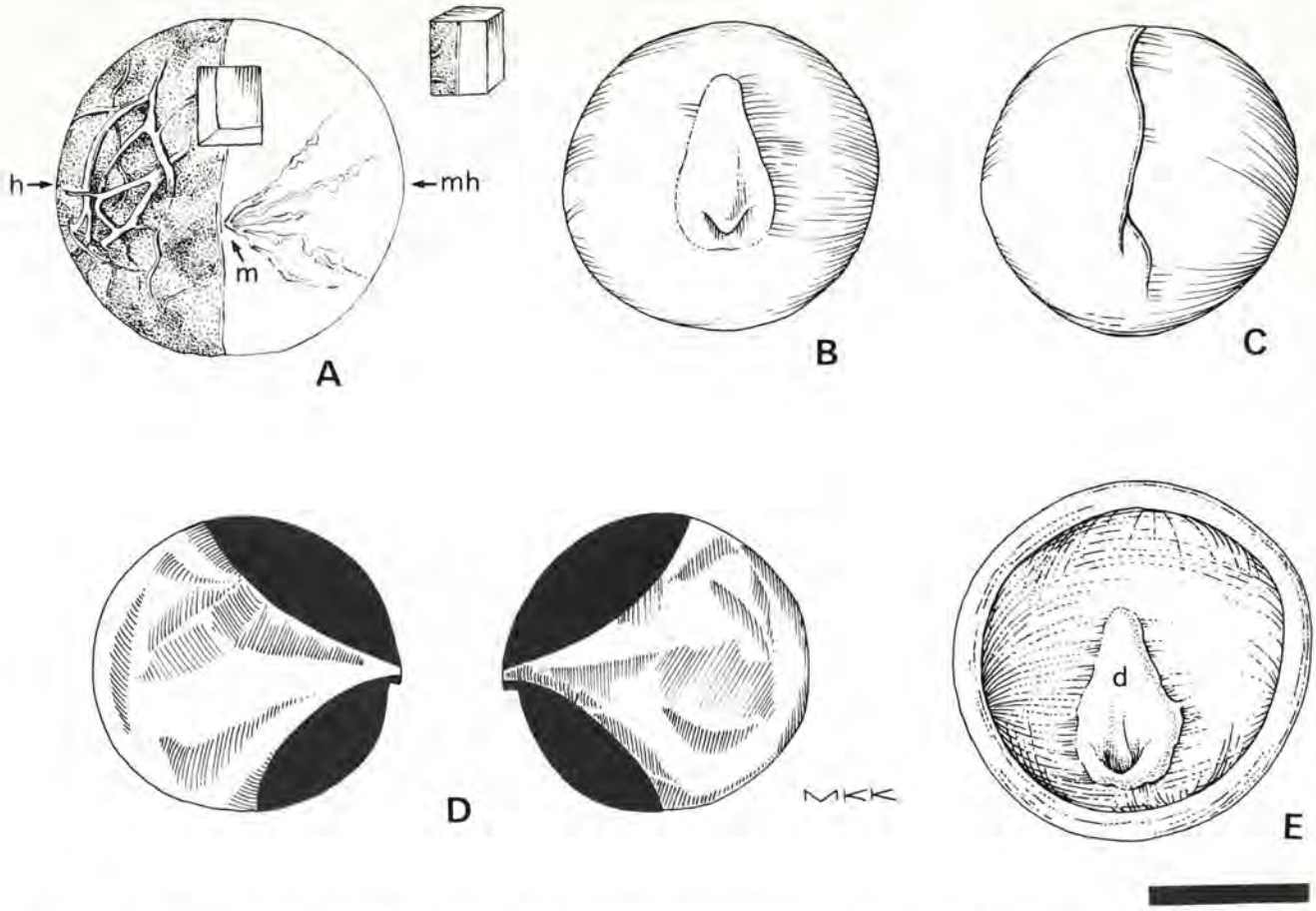


Figure 10A – E Morphology of seed type Y. Mature seed of *E. zeyheri* (*Van Wyk* 3134). A. Seed with part of testa removed showing embryo beneath — note remains of placental tissue (vascular bundles) on hilar hemisphere and wedge-shaped patch of mottled testa (reflecting the position of the depression 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

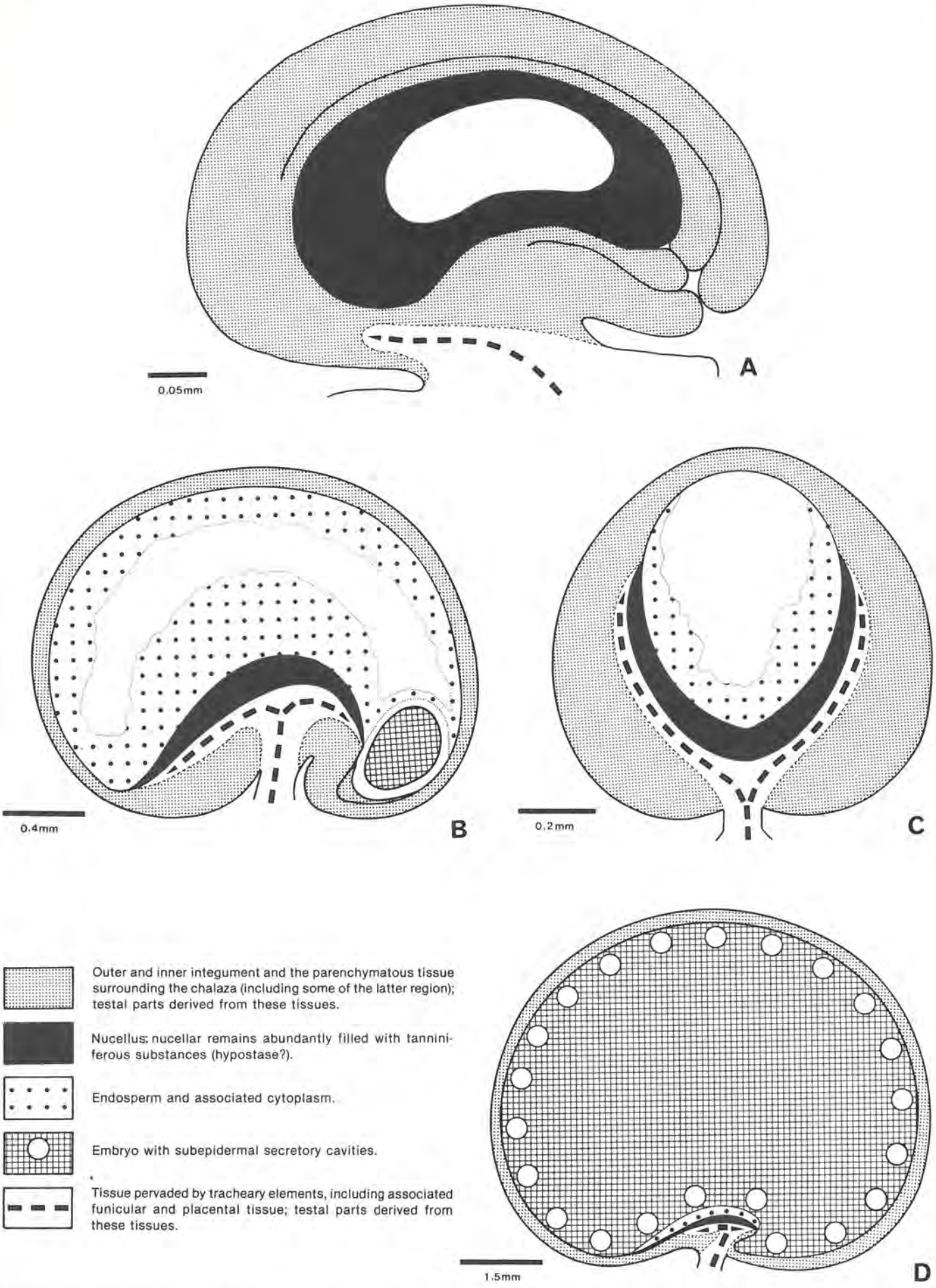


Figure 11A – D Ontogeny of seed type X. Successive stages of seed development in *E. simii* (*Van Wyk* 3296). A. Ovule, longitudinal section. B & C. Very young seed in longitudinal (B) and transverse (C) section — note remains of inner integument persisting in the micropylar region (compare Figures 13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

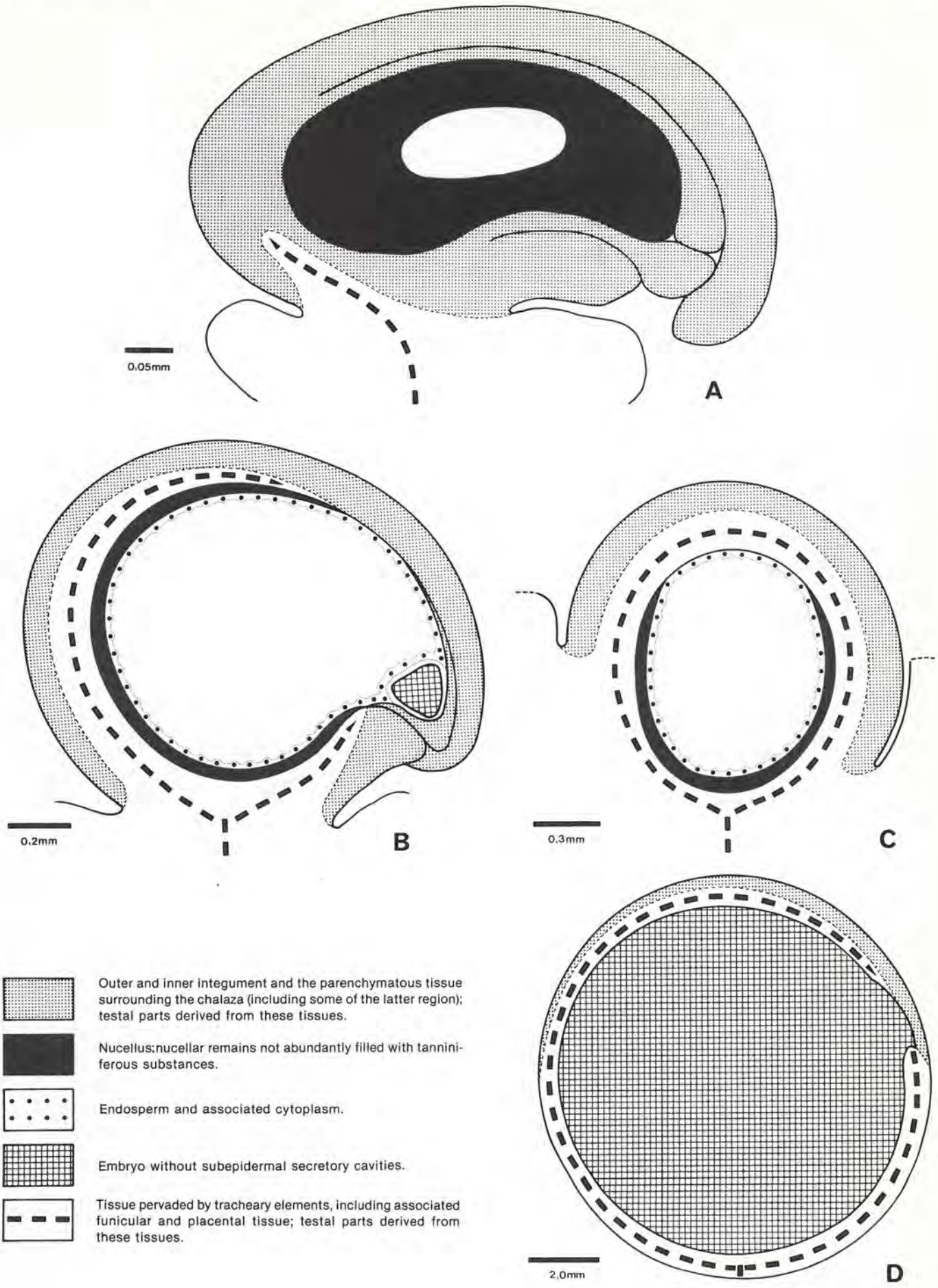
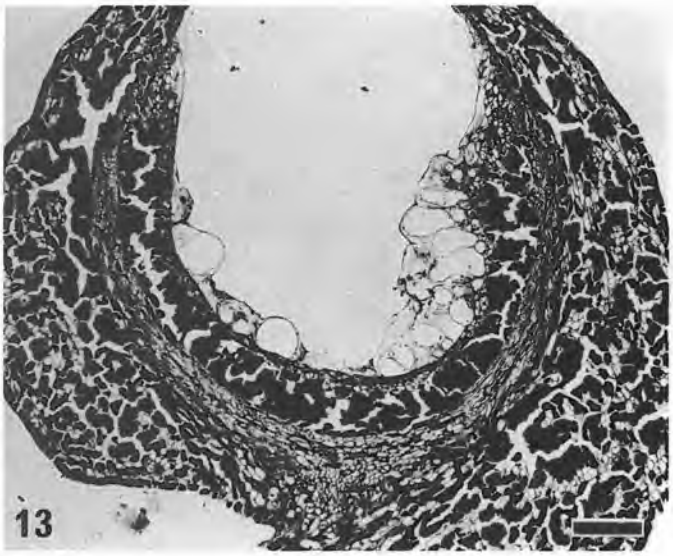
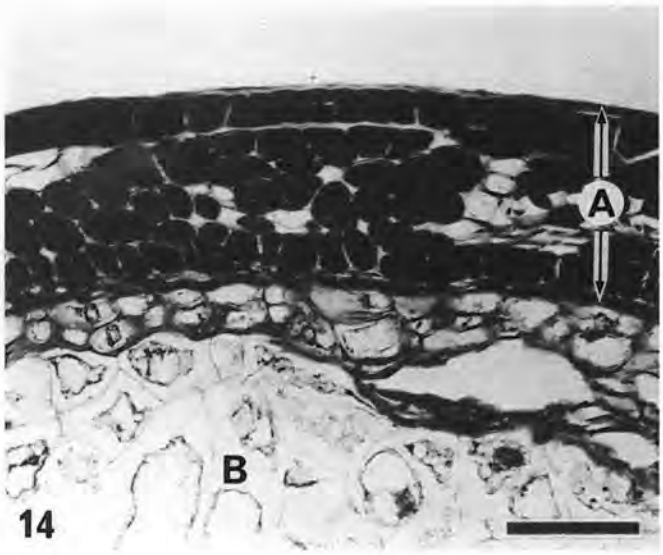
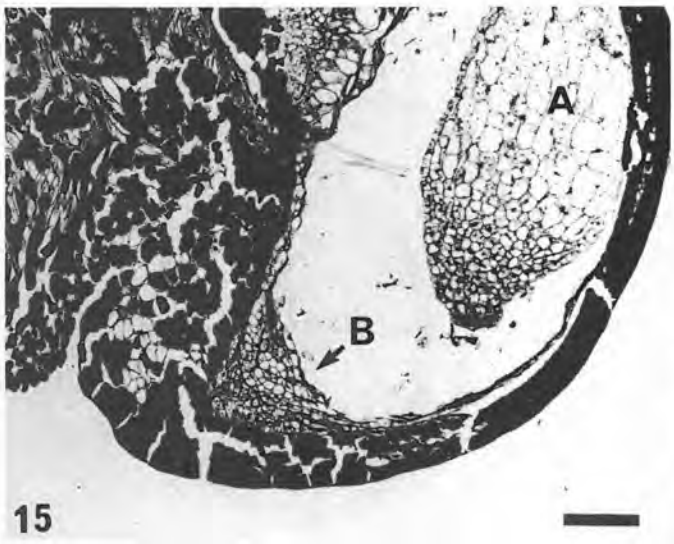
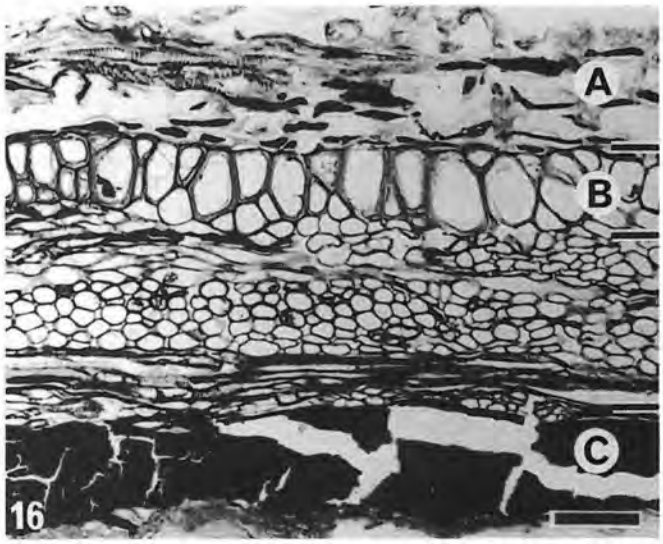


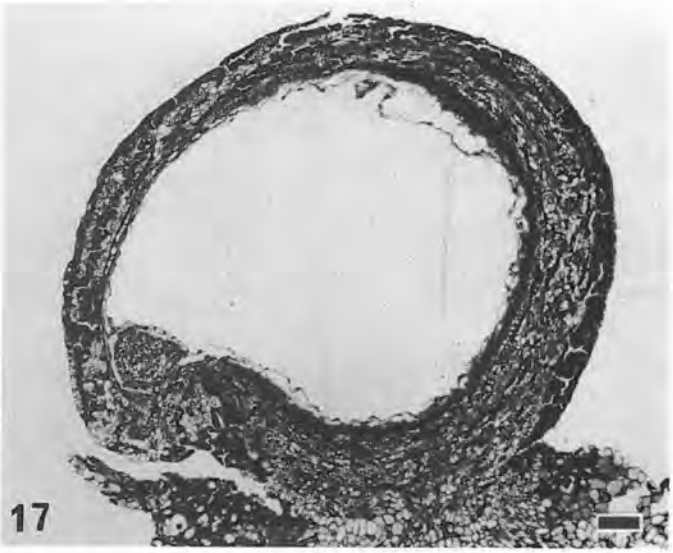
Figure 12A – D Ontogeny of seed type Y. Successive stages of seed development in *E. zeyheri* (*Van Wyk* 3134). A. Ovule, longitudinal section. B & C. Very young seed in longitudinal (B) and transverse (C) section — note remains of inner integument persisting in the micropylar region (compare Figure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

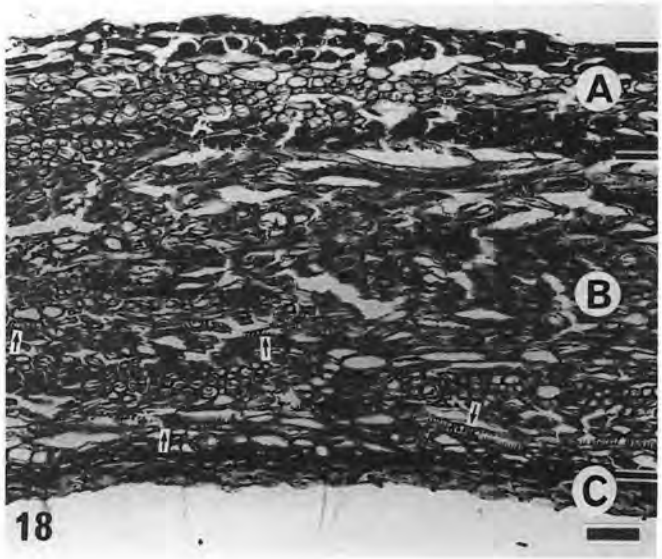




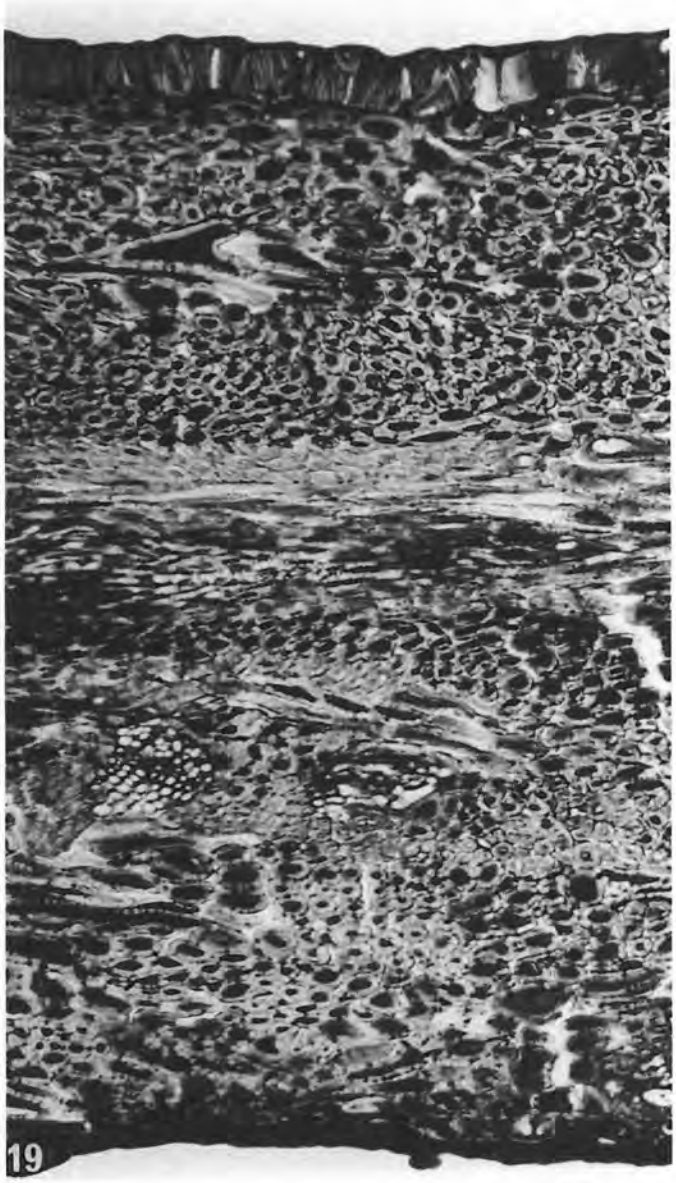


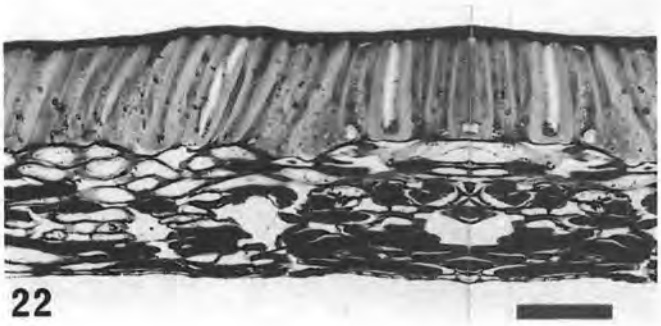


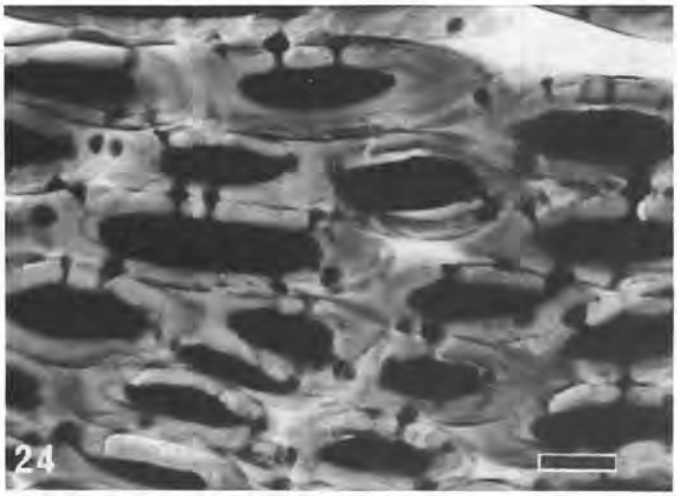




Figures 13 – 18 Morphology of the young seed. 13. *E. simii*, transverse section — compare with Figure 11C. 14. *E. simii*, longitudinal section showing the structure of the testa (A) and endosperm (B). 15. *E. simii*, longitudinal section showing the micropylar region — note embryo (A) and remains of 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).







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.

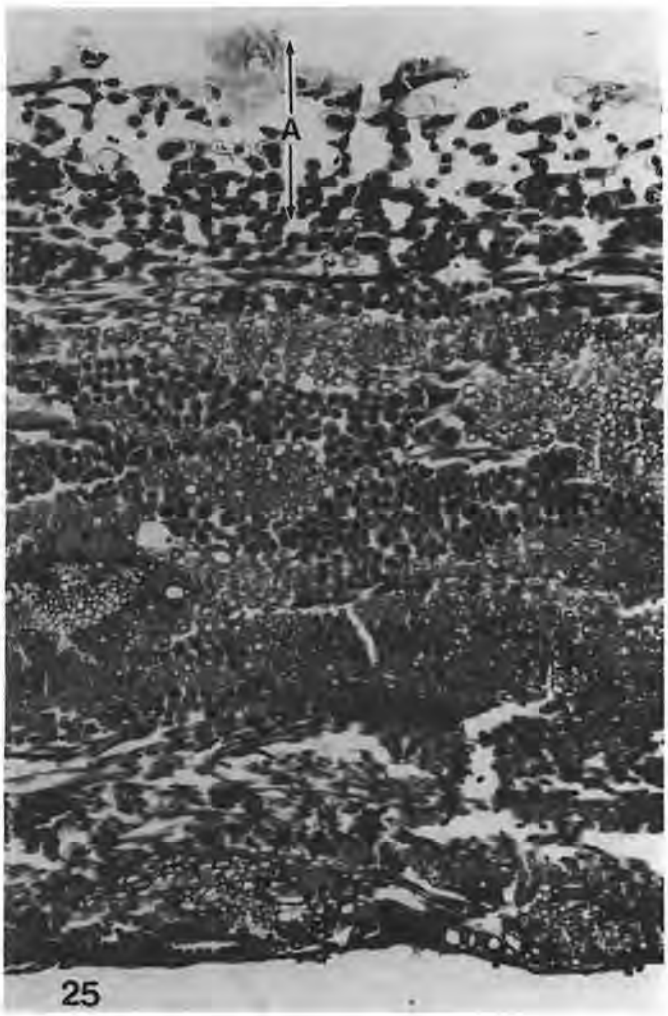
Endosperm formation is nuclear. The young seed cavity (before enlargement of the embryo) is almost completely filled with endosperm (Figures 11B & C, 13 & 14). Eventually the endosperm nuclei are apparently all separated by walls. Most of the endosperm is absorbed by the growing embryo, however, it is 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).

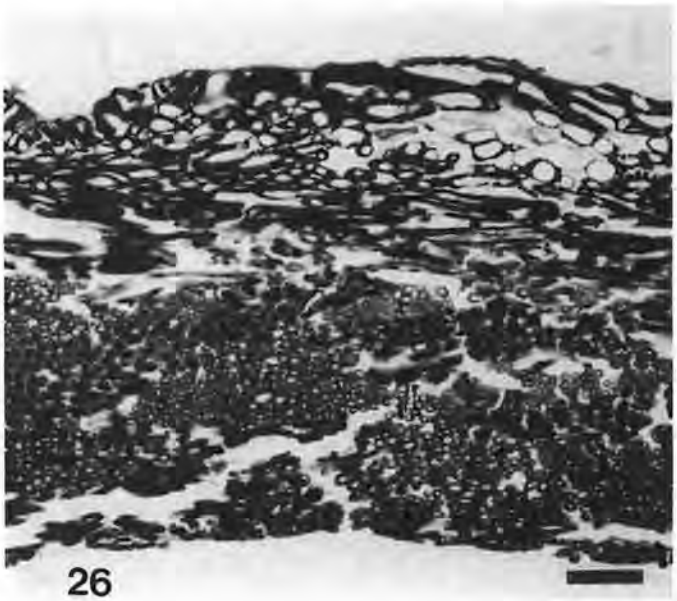
3.3 Ontogeny of seed type Y

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.

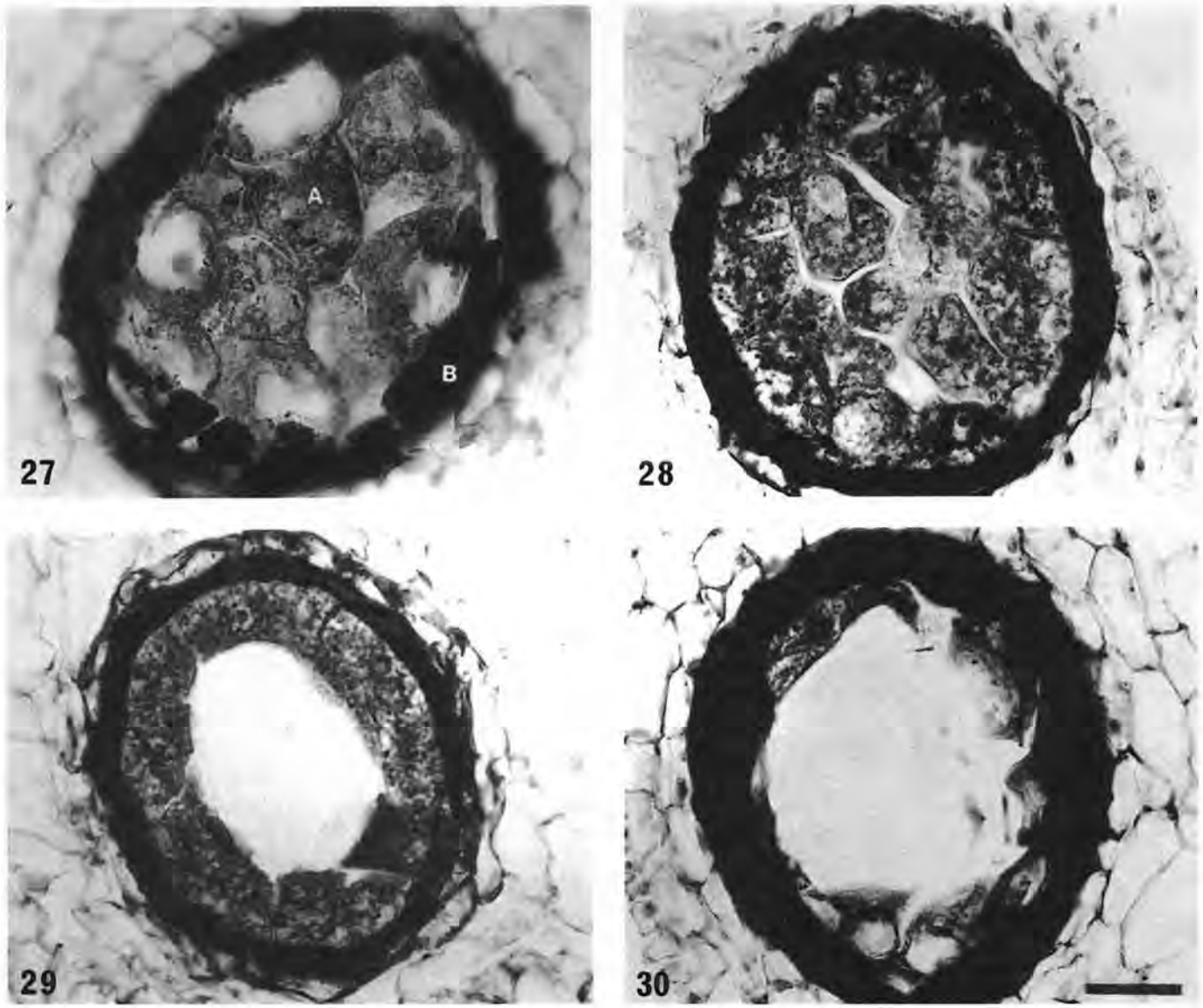
The mature testa is rather thick and woody (cartilaginous?). It develops partly from the outer integument and the chalaza (Figure 12B & C). The inner integument is crushed although the micropylar part lasts slightly longer. During development the nucellus is gradually resorbed by the extended embryo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





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.

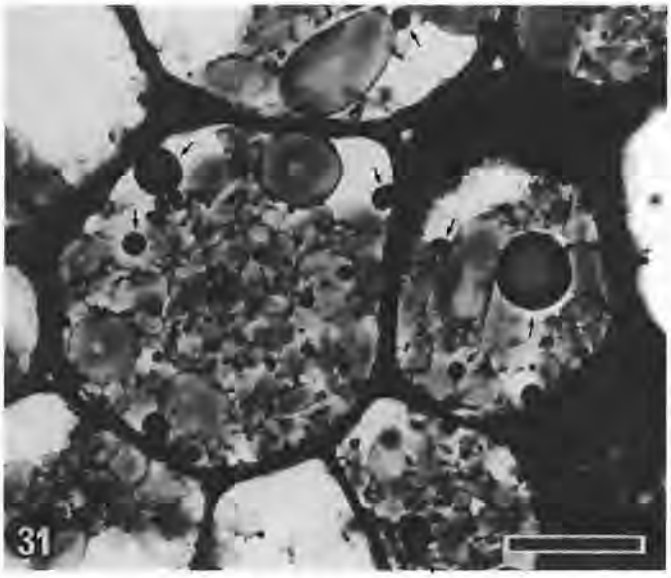


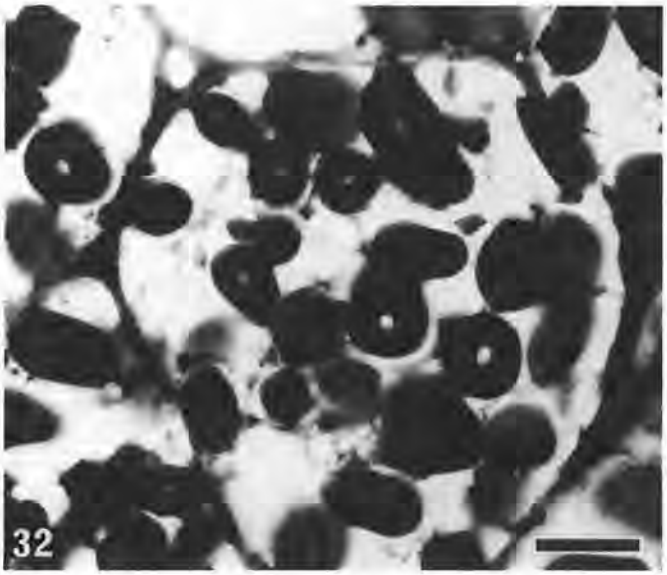
Figures 27 – 30 Stages in the development of secretory cavities in embryo of seed type X. Transverse sections of cotyledons of *E. capensis* (*Van Wyk* 2343). 27. Young secretory cavity with central epithelial cells (A) surrounded by casing cells (B). 28. Interior walls between epithelial cells separating 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-TB. 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 inciden-

tally 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 *Myrciariopsis 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 radicular 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 schizo-

genously, 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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CHAPTER 5

STRUCTURE AND TAXONOMIC VALUE OF WOOD

The genus *Eugenia* (Myrtaceae) in southern Africa: Structure and taxonomic value of wood

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The anatomy of 56 wood samples representing 11 native species of *Eugenia s. str.* was studied. Wood structure is described in detail with emphasis on the taxonomic value of qualitative and quantitative characteristics.

Features observed in most samples include: wood diffuse-porous; pores solitary; perforation plates simple; vestured pits in vessel elements of Van Vliet's type B; vascular and vasicentric tracheids; fibre tracheids with vestured pits; axial parenchyma apotracheal; rays heterogeneous type I and II; ray-vessel pitting small and rounded; chambered axial parenchyma cells with prismatic crystals enclosed by a thick lignified sheath; intracellular deposits of tanniniferous substances; starch grains hollow; no visual distinction between heartwood and sapwood.

Pith flecks were occasionally present and limited gummosis of pith fleck parenchyma resulted in the formation of gum veins. Crystalliferous chains in pith flecks resemble those of the secondary phloem.

The wood anatomy of the species studied largely resembles that of *Eugenia* in other parts of the world and is quite distinct from that of *Syzygium*. No single characteristic or combination of characteristics could be found to be diagnostic at species level. Features that might be useful to distinguish between some species are average pore diameter and lack of tannin in ray cells.

S. Afr. J. Bot. 1983, 2: 135 – 151

Die anatomie van 56 houtmonsters verteenwoordigend van 11 inheemse *Eugenia s. str.*-spesies is ondersoek. Die houtstruktuur word in besonderhede beskryf met klem op die taksonomiese waarde van kwalitatiewe en kwantitatiewe kenmerke.

Kenmerke wat by die meeste eksemplare waargeneem is, sluit onder andere in: hout difuus-poreus; vate uitsluitlik alleenstaande; perforasieplate enkelvoudig; beklede stippels van houtvatelemente is van Van Vliet se tipe B; trageïede en vasisentriese trageïede; veseltrageïede met beklede stippels; aksiale parenchiem apotrageaal; strale heterogeen tipe I en II; straal-houtvatstippeling klein en rond; gekamerde aksiale parenchiemselle met prismatiese kristalle omsluit deur 'n dik gelignifiseerde skede; intrasellulêre tannienneerslae; styselkorrels hol; geen sigbare onderskeid tussen kern- en spinthout.

Murgvlekke was soms teenwoordig en beperkte vergomming van die murgvlakparenchiem gee aanleiding tot die vorming van gomstrale. Kristalhoudende selle in die murgvlekke stem met soortgelyke selle in die sekondêre floëem ooreen.

Die houtanatomie van die ondersoekte spesies stem grootliks ooreen met dié van *Eugenia* in ander wêrelddele en verskil opvallend van dié van *Syzygium*. Geen kenmerk of kombinasie van kenmerke wat diagnosties is op spesievlak, is gevind nie. Kenmerke wat wel handig kan wees om tussen spesies te onderskei, is gemiddelde vaatdeursnee en afwesigheid van tannien in vaatstraalselle.

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Keywords: Crystals, *Eugenia*, Myrtaceae, pith flecks, wood anatomy

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1. Introduction

This study forms part of a project on the comparative morphology and anatomy of the southern African species of *Eugenia*. The principal aim is to evaluate the taxonomic potential of various characteristics as an aid towards a regional revision of this taxonomically difficult genus. Aspects already dealt with include the anatomy of leaves and twigs (Van Wyk 1978), structure of the first-formed stem periderm (Van Wyk *et al.* 1980), structure of stomata (Van Wyk *et al.* 1982), seed morphology (Van Wyk 1980) and some aspects of foliar leaf organography (Du Plessis & Van Wyk 1982). The most useful finding thus far is probably the recognition of characteristics facilitating a distinction between two groups of species. These supraspecific groups are tentatively referred to as Groups X and Y.

Wood appears to be the most conservative part of the plant. It is therefore not surprising that wood features are not frequently diagnostic at the species level (Metcalfe & Chalk 1950; Barefoot & Hankins 1982). However, in some instances wood anatomy of the Myrtaceae does reveal many consistent, clear-cut anatomical features that are of value at the generic level (Ingle & Dadswell 1953). But strangely enough, with the exception of ray types (Ingle & Dadswell 1953) there appear to be no consistent differences between the wood of the Myrtoideae and Leptospermoideae (Solereder 1908; Metcalfe & Chalk 1950).

Wood of the southern African species of *Eugenia* shows little commercial potential and has been exploited only to a very limited extent in the past. This could be one of the reasons for the lack of previous studies on the structure of the mature wood of the group. Juvenile xylem from twigs of the southern African *E. capensis* (Eckl. & Zeyh.) Sond. and *E. albanensis* Sond. was studied by Dadswell & Ingle (1947) and that of most native species of *Eugenia* by Van Wyk (1978). Dadswell and Ingle gained support from the wood anatomy for the subdivision of *Eugenia s. l.* proposed by Merrill & Perry (1938). They concluded that the wood anatomy of the two southern African species resembles that of *Eugenia s. str.* which is mainly restricted to the New World. This view was confirmed by Van Wyk (1978), although no constant interspecific features could be demonstrated. Kromhout (1975, 1977) described the mature wood anatomy of *E. zeyheri* Harv., *Syzygium cordatum* Hochst. and *S. gerrardii* (Harv. ex Hook. f.) Burtt Davy.

This paper reports the first comparative anatomical study of the mature wood of the southern African species of *Eugenia*. It was carried out to provide a detailed description of the wood structure with emphasis on the taxonomic value of the characteristics.

2. Material and Methods

Wood samples of 11 native species of *Eugenia* were studied by means of light and scanning electron microscopy (SEM). Samples from two taxa probably representing unnamed species were also included. These are referred to as *Eugenia* spp. A and B. Material from the rhizomatous geoxylic suffrutices, *E. albanensis, E. pusilla* N.E. Br. (probably extinct) and *E.* cf. *mossambicensis* Engl. (probably a form of *E. capensis*) were excluded. Studied specimens and herbarium vouchers are listed in Table 1. All collection numbers are those of the first author and voucher specimens are kept in the H.G.W.J. Schweickerdt Herbarium (PRU), University of Pretoria. Localities are given as quarter-degree grid references (Edwards & Leistner 1971).

With the exception of the multi-stemmed shrub, *E. simii*, wood samples were taken at 0,5 m height from more or less vertical stems not less than 8 cm in diameter. Samples of *E. simii* were taken from stems 3 – 6 cm in diameter at a position usually less than 0,5 m high. Samples were fixed in F.A.A.

For light microscopy wood samples were softened with steam and cut with a sliding microtome. Sections *ca.* 15 μm thick were stained with safranin O, counter-stained with fast green FCF (Johansen 1940) and mounted in the xylene-based mountant Entellan. Macerates were prepared by carefully heating test tubes containing slivers of wood submersed in Schulze's solution (McLean & Cook 1941) in a water bath at ± 60 °C. The macerated material was thoroughly washed with water, stained with safranin 0 and mounted in Entellan. The slides are housed in the slide collection of the Department of Botany, University of Pretoria and a duplicate set in the Department of Wood Science, University of Stellenbosch. The slide numbers correspond to the collection numbers of voucher specimens.

For SEM studies both clean-cut and fractured wood samples, exposing tangential or radial surfaces, were used. Fractured surfaces are particularly useful for studying the vestured pit chambers, while clean-cut surfaces permit easy examination of the intravascular pit apertures. After cutting or splitting, wood samples of about 5 mm^{-2} were thoroughly washed in water, soaked for about 30 minutes in a 20% solution of sodium hypochlorite to remove most of the cytoplasmic debris from the surface cells, again washed with water and air dried (Exley *et al.* 1974, 1977). The dried samples were mounted on stubs, sputter-coated with gold and examined with the SEM.

The following procedure was followed to obtain sections of starch grains. Pieces of wood were thoroughly washed in water to remove all traces of fixative. Starch grains were collected by scraping a tangential or radial wood surface with a razor blade. The collected pulp-like material (obviously also containing cells and cell remnants) was dried on a hot plate (50 °C) and crushed with a glass rod. A small amount of this powdered material was mixed with a few drops of 1,2-propylene oxide in a BEEM embedding capsule. After most of the propylene oxide had evaporated (a few minutes), the capsules were filled with Spurr's resin (Spurr 1969), left open for at least 24 hours in a desiccator and polymerized at 70 °C. Sections 0,5 – 1 μm thick were cut on an ultra microtome, mounted in potassium iodide-iodine (IKI) (Johansen 1940) and examined with a light microscope.

All measurements were made with a MOP-AMO 3 Kontron image analyzer combined with a projection microscope. Descriptive terms and standards for the determination of characteristics (except pore diameter) follow the recommendations of the International Association of Wood Anatomists (IAWA Committee 1964, 1981).

Tangential pore diameter was measured on a transverse section traversed in a radial direction. To obtain the average tangential diameter, 100 pores were measured on each specimen and the total averaged. The 25 largest measurements of these 100 were used to calculate the average maximum tangential diameter.

3. Results and Discussion

3.1 General wood anatomical description of the southern African species of *Eugenia*

Growth rings distinct. Wood predominantly diffuse-porous (rarely appearing semi-ring-porous). *Pores* solitary, 10 – 90 mm^{-2}, round to oval, average tangential diameter 38 – 73 μm, average maximum tangential diameter 50 – 90 μm. Vessel members with short to long tails. Length (including tails) (180)380 – 870(1130) μm. Occasionally with tanniniferous deposits. Perforation plates exclusively simple and usually oblique. Tyloses small and sparse, occasionally large and sclerotic, usually tanniniferous. Vessel-ray and vessel-parenchyma pits half-bordered. Pits alternate to opposite, round, 3 – 6 μm in diameter, chambers predominantly vestured. Vestures mostly of Van Vliet's type B. *Vascular tracheids* rarely present and sparse. *Vasicentric tracheids* present although sparse and apparently absent in some samples. *Fibres* with pits mostly conspicuously bordered (fibre tracheids), (570)760 – 1440(2210) μm long. Cell walls vary from thick to very thick. Inner pit apertures included. Pit chambers often vestured. *Axial parenchyma* apotracheal, usually diffuse or diffuse-in-aggregates, sometimes in fine lines or occasionally tending to be narrowly banded. Strands of (1)5 – 12(20) cells. *Rays* heterogeneous, types I & II; with one or usually more than one row of upright cells; procumbent portion (1)2 – 3(5) cells wide. Uniseriate rays of only upright cells always present. Multi-seriate rays sometimes vertically fused. Ray cells thick-walled and abundantly pitted; upright cells frequently disjunctive. Average height of procumbent portion of ray 85 – 250 μm. Ray cell height (10)12 – 14(16) μm. Number of rays per mm (14)18 – 25(30). *Axial intercellular canals* of the traumatic type (gum veins) frequently present and developing from pith flecks. Associated parenchyma cells predominantly tanniniferous, usually with abundant starch grains; brachysclereids, fibres and strands of crystalliferous cells occasionally present. Intercellular deposits of gum usually present in short tangential lines. *Crystals* always prismatic, frequent in axial parenchyma; single or in crystal-

Table 1 Voucher specimens and selected quantitative wood features

Specimens examined and specimen numbers[a]	Grid reference	Pores: Average tangential diameter (μm)	Pores: Average maximum tangential diameter (μm)	Pores: Number /mm²	Average height of procumbent portion of ray (μm)
Group X					
E. capensis (Eckl. & Zeyh.) Sond.					
2586	2831 DD Nkandla	71	82	28	142
4510	3030 CB Port Shepstone	67	82	28	145
2619	3130 AA Port Edward	64	77	30	125
2618	3130 AA Port Edward	69	80	41	85
4507	3030 BB Port Shepstone	67	80	25	126
4508	3030 BB Port Shepstone	71	83	24	101
4509	3030 BB Port Shepstone	73	90	22	95
E. natalitia Sond.					
950	2732 AC Ubombo	55	67	26	138
2793	2230 CD Messina	65	78	25	237
2794	2230 CD Messina	59	71	31	241
4252	2930 DD Pietermaritzburg	53	65	49	130
4254	3030 BC Port Shepstone	56	65	27	115
4286	2329 BB Pietersburg	64	78	38	153
E. simii Duemmer					
1269	3030 CA Port Shepstone	41	54	30	182
1270	3030 CA Port Shepstone	49	64	30	165
4243/1	3030 CA Port Shepstone	46	61	28	124
4243/2	3030 CA Port Shepstone	48	62	47	156
4516	3030 CA Port Shepstone	44	55	20	135
4519	3030 CD Port Shepstone	48	60	35	120
4520	3030 CD Port Shepstone	51	65	17	124
E. umtamvunensis Van Wyk					
3631	3030 CC Port Shepstone	63	76	20	214
4232	3030 CC Port Shepstone	61	75	27	244
Group Y					
E. erythrophylla Strey					
1698	3030 CC Port Shepstone	70	80	17	190
3342	3030 CC Port Shepstone	67	80	15	152
4511	3030 CC Port Shepstone	68	80	35	120
E. verdoorniae Van Wyk					
1696	3030 CC Port Shepstone	73	91	18	152
4512	3030 CC Port Shepstone	58	72	21	143
2335	3030 CC Port Shepstone	51	63	27	163
2334	3030 CC Port Shepstone	66	83	16	120
E. woodii Duemmer					
2517	2732 AC Ubombo	72	88	19	219
2522	2732 AC Ubombo	57	72	40	125
2659	3030 BC Port Shepstone	63	76	30	180
4255	3030 BC Port Shepstone	56	68	26	103
2805	2230 CD Messina	60	77	19	133
2973	2230 CD Messina	58	72	12	128
4061	2230 CD Messina	71	89	27	243
E. zeyheri Harv.					
3126	3227 AC Stutterheim	46	56	33	171
3127	3227 AC Stutterheim	54	68	32	173
3134	3326 BD Grahamstown	47	61	48	128
3135	3326 BD Grahamstown	38	46	62	159
3163	3326 DB Grahamstown	40	51	21	160
3189	3325 BC Port Elizabeth	42	51	31	203
E. zuluensis Duemmer					
2662	2929 BD Underberg	46	59	42	245
2663	2929 BD Underberg	46	55	29	144
2664	2929 BD Underberg	51	67	42	214
3263	3029 DA Kokstad	55	69	31	155
3264	3029 DA Kokstad	49	61	37	248
3267	3029 DA Kokstad	52	68	34	166
3268	3029 DA Kokstad	46	57	30	185
E. sp. A					
2630	3030 CA Port Shepstone	43	52	46	154
4244/1	3030 CA Port Shepstone	39	52	51	165
4244/2	3030 CA Port Shepstone	39	50	79	138
4513	3030 CA Port Shepstone	45	58	88	171
4514	3030 CA Port Shepstone	44	55	46	141
4515	3030 CA Port Shepstone	42	53	67	176
E. sp. B					
2629	3030 CA Port Shepstone	47	62	42	199

[a]Bracket signifies wood samples from the same population

liferous chains of variable length; one crystal per cell or chamber. Crystals integumented. Integument usually thickened, lignified and resembling the cell wall. *Starch granules* hollow, simple or 2(3)-compound. *Miscellaneous features:* no visual distinction between heartwood and sapwood is noticeable. Wood colour pale brown often with a tinge of pink or yellow. Basic specific gravity 0,65 – 0,9. Splinter burns to a grey or white (rarely black) ash.

3.2 Additional notes and discussion of wood anatomical features

(a) *Growth rings and vessels*

As a result of the following late wood features, growth rings are more or less clearly distinguishable in the wood of southern African species of *Eugenia*: smaller and denser fibres; less axial parenchyma; fewer and smaller pores; more tanniniferous rays (Figures 1, 2, 3, 4 & 31).

The lack of pores in bands of late wood creates the impression of semi-ring-porous wood in some specimens (Figure 2). However, these areas are usually restricted to parts of a section or wood sample and the wood of all species is predominantly diffuse porous.

Vessels (Figures 19 & 22), partly or completely filled with tanniniferous substance, are occasionally present in all species (Figure 5). These vessels are particularly abundant in parts of the wood of *E. natalitia*.

Tyloses are rare, usually small and tanniniferous. Vessels completely blocked with sclerosed tyloses are infrequent and usually close to pith flecks (Figure 6). Sclerosed tyloses have not previously been reported in *Eugenia*.

The number of pores per mm^2 (Table 1) and the length of vessel members are extremely variable and of no diagnostic value.

The average tangential and average maximum tangential diameters of the pores are given in Table 1. In a species, pore diameter is often remarkably similar for different wood samples from the same (e.g. *E. erythrophylla*) or different (e.g. *E. capensis*) populations. However, a large variation occurs among samples in other species such as *E. verdoorniae* and *E. zeyheri*. In species belonging to Group X, there is a tendency for the average pore size to be relatively large in *E. capensis* (64 – 73 μm) and small in *E. simii* (41 – 51 μm). The average pore diameter in Group Y tends to be relatively large in *E. woodii* (56 – 72 μm) and small in *E. zeyheri* (38 – 54 μm) and *E.* sp. A (39 – 45 μm). The small pores in the last two species may be taxonomically significant in the light of other morphological similarities between them. Despite these tendencies, pore size is too variable to be diagnostic for most of the species.

The variability of mainly quantitative anatomical wood features in Myrtaceae was clearly illustrated in a comprehensive study of *Metrosideros* Banks in Hawaii (Sastrapradja & Lamoureux 1969). These authors could find no single characteristic nor a combination of characteristics to differentiate between the wood of 12 taxa studied. Nor could they find any correlation between these characteristics, annual rainfall and altitude.

Dimensional variation and structure of the vessels in southern African species of *Eugenia* are well within the limits recorded for *Eugenia s. str.* in other parts of the world (Record & Hess 1949; Metcalfe & Chalk 1950; Ingle & Dadswell 1953).

(b) *Tracheids and fibre tracheids*

Tracheid-like elements are very sparse in macerations and what appears to be vasicentric tracheids are occasionally present. However, an assessment of this feature is very difficult because varying degrees of gradation exist from vasicentric tracheids to fibre tracheids.

Vasicentric tracheids have been reported to be common in the wood of *Eugenia* in other parts of the world (Dadswell & Ingle 1947; Record & Hess 1949; Ingle & Dadswell 1953) and in fact throughout the Myrtaceae (Metcalfe & Chalk 1950) with the exception of *Acmena* DC., *Cleistocalyx* Blume, *Syzygium* Gaertn. (all Myrtoideae), *Eucalyptopsis* White and *Piliocalyx* Brongn. & Gris. (Leptospermoideae) (Ingle & Dadswell 1953). The presence of these cells is taxonomically important in Myrtaceae and features prominently in an anatomical key to 32 genera of the Myrtaceae in the South-West Pacific area (Ingle & Dadswell 1953). Despite its reputed diagnostic value, observations on the wood of *Eucalyptus* have shown that these elements can range in quantity from very sparse to abundant within the same species (Dadswell 1972). Its infrequent occurrence in some wood samples of *Eugenia* in southern Africa is consequently treated as a normal variation.

Fibres are thick- to very thick-walled (Figures 7 & 8) and non-septate, usually with distinctly bordered pits and therefore are fibre tracheids, often containing vestures (see 3.2(g)). The bordered pits (Figures 9, 11 & 12) are evenly distributed between both radial and tangential walls. Fibre tracheids are frequent in Myrtaceae (Metcalfe & Chalk 1950) although the lack of conspicuously bordered pits is one of the anatomical wood features employed by Dadswell & Ingle (1947) and Ingle & Dadswell (1953) to separate *Syzygium* and a number of smaller genera from *Eugenia s. str.*

Tanniniferous fibre tracheids are sparse and often associated with tanniniferous vessel elements (Figure 10). Fibre length is rather constant within a sample but shows no constant interspecific differences.

(c) *Axial parenchyma*

Apotracheal parenchyma is usually present in axial strands of more than eight cells. Starch grains are abundantly present. Cells are usually not tanniniferous. If present, however, tanniniferous cells are usually restricted to certain areas in a wood sample or to specific growth rings (Figure 3). Crystals are present, often in abundance (see 3.2(f)). No constant interspecific differences were noticed.

The presence of apotracheal axial parenchyma in *Eugenia s. str.* and paratracheal parenchyma in *Syzygium* was employed by Dadswell & Ingle (1947) and Ingle & Dadswell (1953) to support the proposal by Merril & Perry (1938) of differentiation between these two genera (previously treated as a single combined genus viz. *Eugenia s.l.*). Axial parenchyma of the southern African *Syzygium* species is also paratracheal (Kromhout 1975) and thus supports its separation from *Eugenia* in this region.

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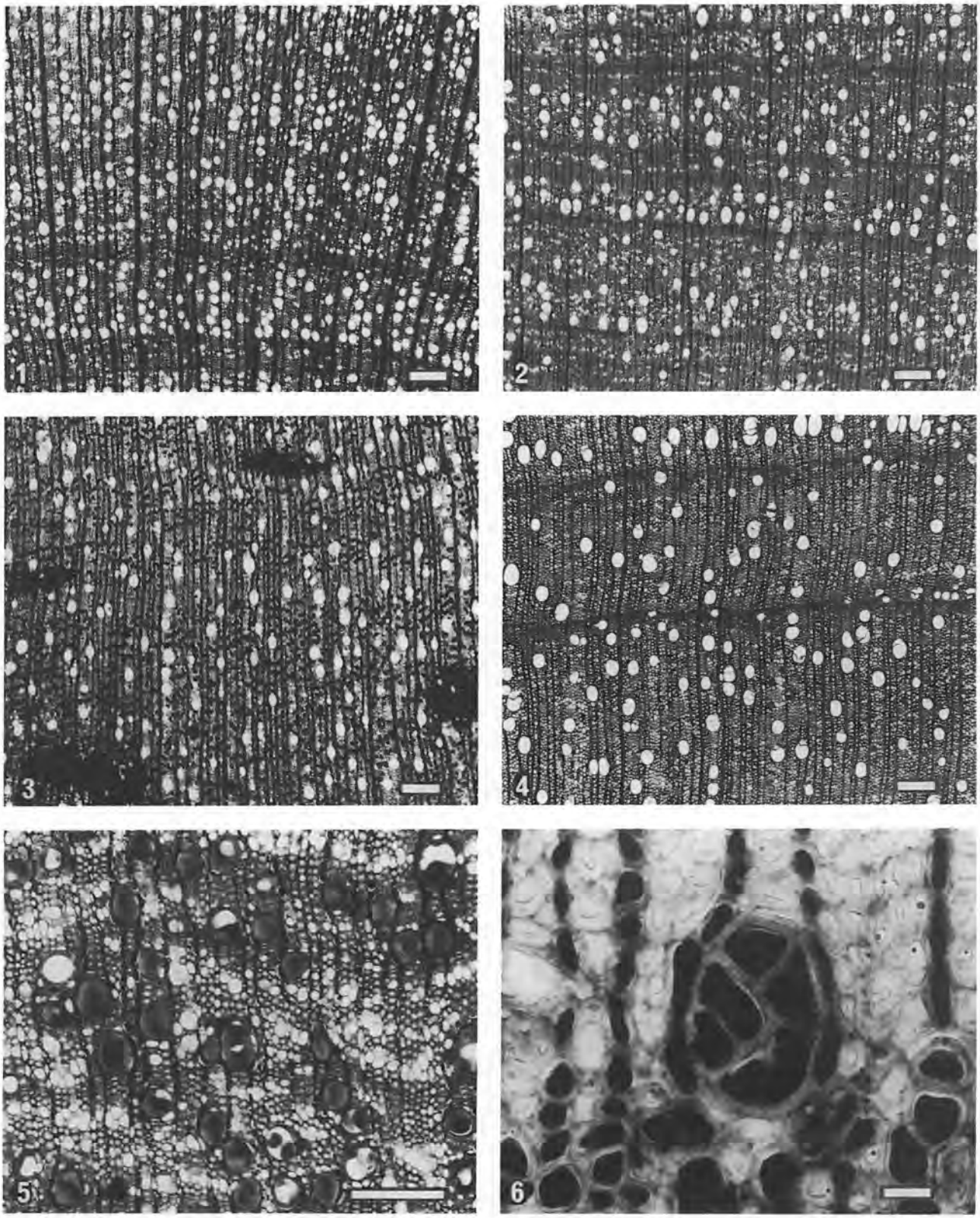
(d) *Rays*

Rays of southern African species of *Eugenia* are either multiseriate and heterogeneous with the central procumbent cells being sharply separated from the marginal square or brick-like upright cells, or uniseriate and then usually composed only of upright cells (Figures 13 – 17). Both these types occur together in all specimens examined. Upright cells are usually greater in axial than in radial dimensions. In tangential section the procumbent cells are circular in outline (Figures 14, 16 & 23). These ray types are typical for many Myrtoideae (Ingle & Dadswell 1953).

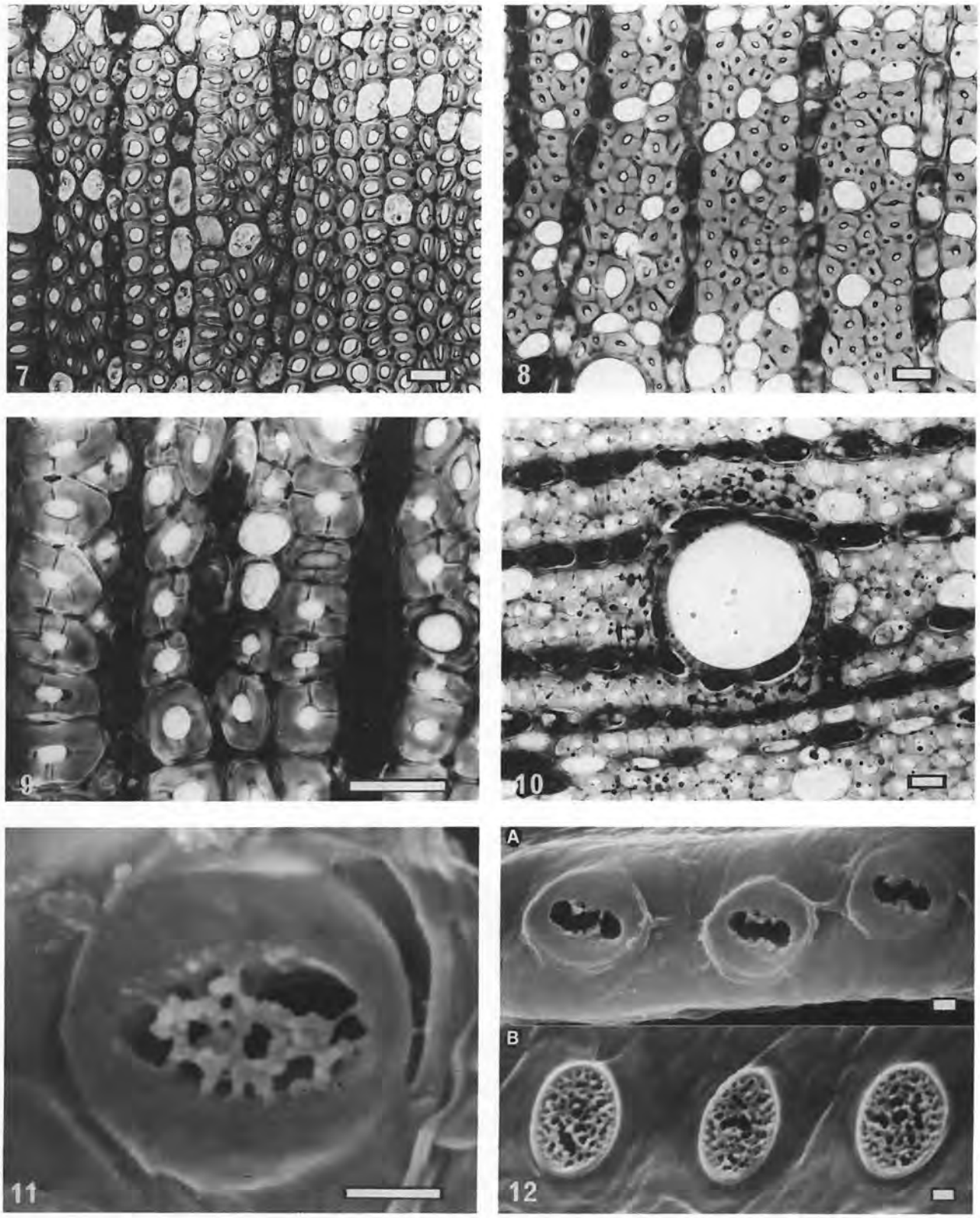
The average height of the procumbent portion of the rays is given in Table 1. No constant interspecific differences for this and other quantitative ray features were noticed.



Figures 1 – 6 Transverse sections. 1. *Eugenia zeyheri* (*Van Wyk, 3135*). 2. *E.* sp. B (*Van Wyk, 2629*). 3. *E. simii* (*Van Wyk, 1269/1*) — note pith flecks and tanniniferous axial parenchyma cells. 4. *E. natalitia (Van Wyk, 4286)*. 5. *E. woodii (Van Wyk, 2522)*. 6. *E. capensis (Van Wyk, 2586)* showing a pore with sclerotic tyloses. Scale line = 200 μm (Figures 1 – 5) or 20 μm (Figure 6).

In contrast to the axial parenchyma, tannin deposits are usually present in the ray cells (Figures 13, 14, 17 & 18). The density of deposits often differs between upright and procumbent cells — thus indicating a possible physiological difference. Ray cells containing very little or no tanniniferous substance in at least the procumbent cells were recorded in three samples of *E.* sp. A and all the specimens of *E. zuluensis* (Figures 15 & 16). More samples need to be studied to ascertain the consistency of this feature in the latter species.

Vessel-ray pitting is small and half-bordered with the diameter of the borders being up to 6 μm. This agrees with



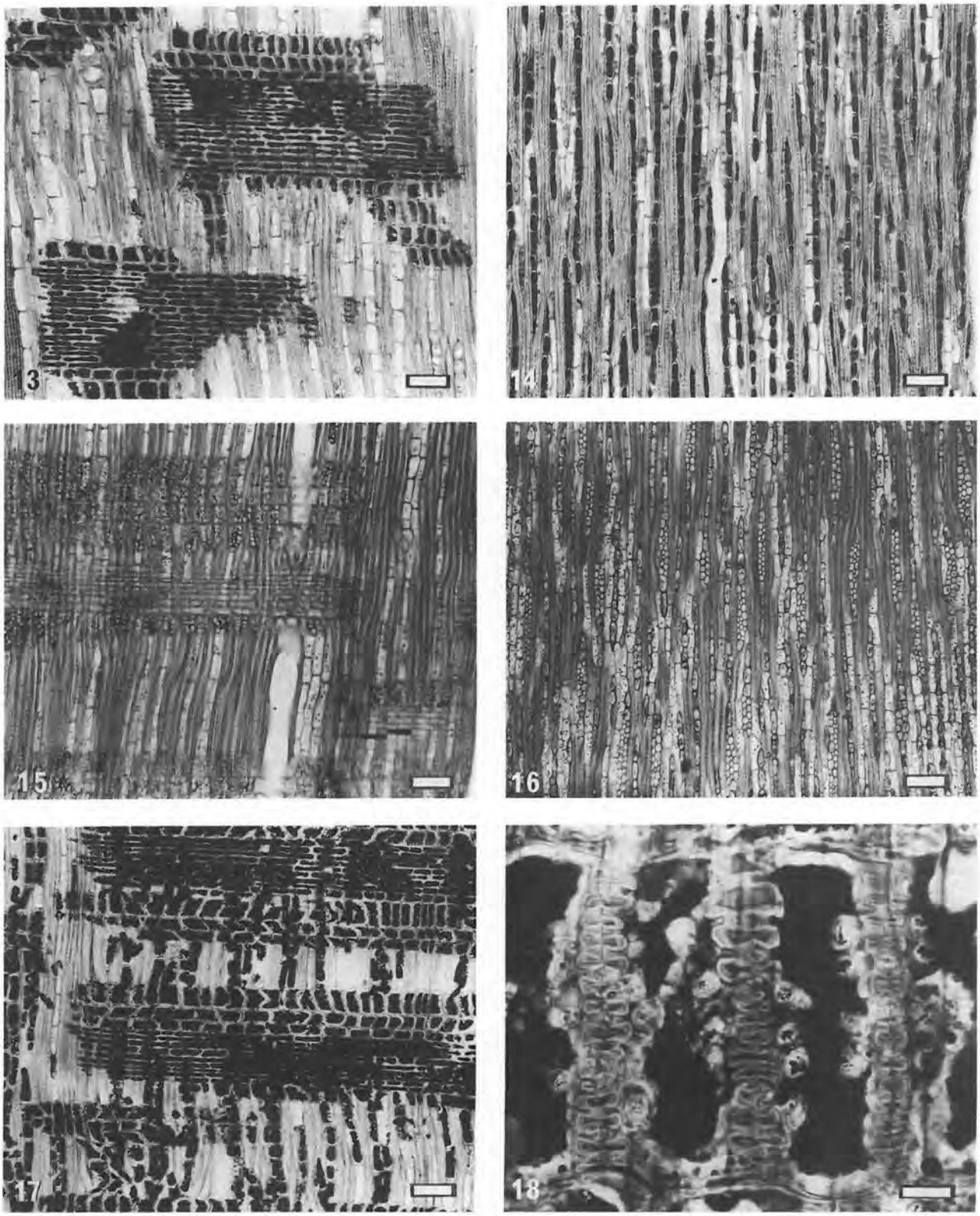
Figures 7 – 12 Morphology of fibre tracheids. 7. Transverse section of *E. capensis (Van Wyk, 4507)* showing thick-walled fibres. 8. Transverse section of *E. zeyheri (Van Wyk, 3135)* showing very thick-walled fibres and 9. conspicuous bordered pits. 10. Transverse section of *E. erythrophylla (Van Wyk, 1698)* showing tanniniferous fibres (vasicentric tracheids?) around pore. 11. SEM micrograph of *E. erythrophylla (Van Wyk, 3342)* showing a fibre vestured pit. 12. SEM micrographs of *E. woodii (Van Wyk, 2517)* comparing vestured pits of fibre (A) and vessel element (B). Scale line = 20 μm (Figures 7 – 10) or 1 μm (Figures 11 & 12).

the vessel-ray pitting in New and Old World *Eugenia* species. Distinctive elongated and often scalariform vessel-ray pits are characteristic for *Syzygium* and allied genera (Dadswell & Ingle 1947; Ingle & Dadswell 1953).

Ray cells are thick-walled and abundantly pitted. The end walls of the upright cells are frequently disjunctive (Figures 18 & 24). This is also characteristic for *Eugenia* in other parts of the world (Dadswell & Ingle 1947; Record & Hess 1949).

(e) *Pith flecks and gum veins*

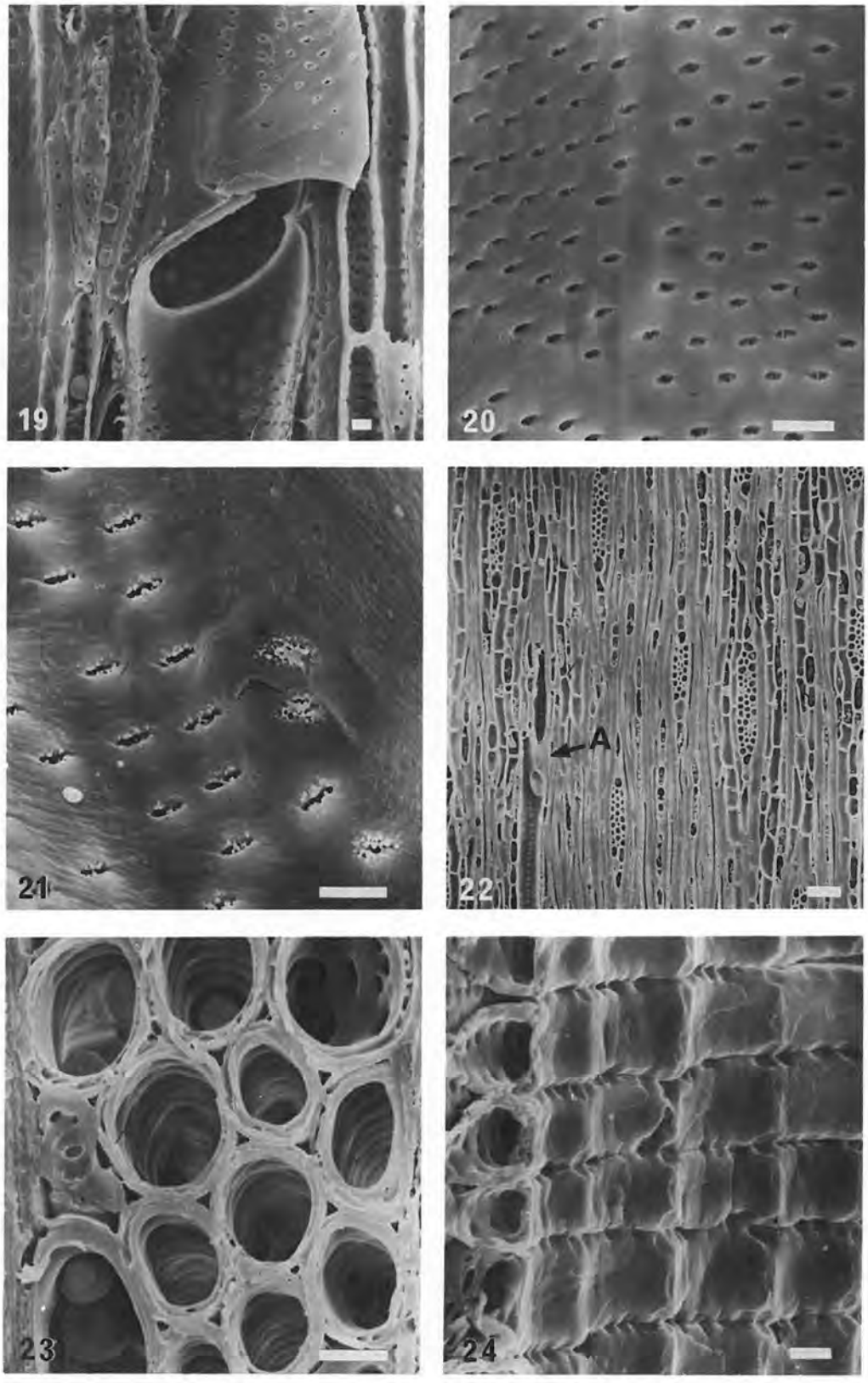
Macroscopic dark brown or black spots are conspicuous on the transverse surface of many wood samples studied. These were especially noticeable in freshly cut live wood. These



Figures 13 – 18 Morphology of rays. 13. Radial section of *Eugenia woodii (Van Wyk, 2805)*. 14. Tangential section of *E. zeyheri (Van Wyk, 3134)*. 15. Radial section of *E. zuluensis (Van Wyk, 2662)* — note abundant starch grains in upright cells. 16. Tangential section of *E. zuluensis (Van Wyk, 2664)* showing ray cells without tanniniferous substance. 17. Radial section of *E. simii (Van Wyk, 1269/1)*. 18. Radial section of *E. woodii (Van Wyk, 2522)* showing disjunctive upright cells. Scale line = 200 μm (Figures 13 – 17) or 10 μm (Figure 18).

short, usually tangentially elongated spots proved to be due to intercellular deposits of a darkly coloured material (gum?) associated with multicellular axial strands of anomalous parenchyma (pith flecks). The parenchyma is quite inconspicuous owing to a lack of colouring matter in the cells.

In Myrtaceae such depository canals (if well developed) are usually referred to as gum or kino veins (Dadswell 1972). They are also known as axial (vertical) intercellular canals of the traumatic or 'gummosis' type (Brazier & Franklin 1961; Barefoot & Hankins 1982), gum ducts/canals



Figures 19 – 24 SEM micrographs of vessels and rays. 19. *Eugenia* sp. B (*Van Wyk, 2629*) showing a simple perforation. 20. *E. umtamvunensis (Van Wyk, 3631)* showing pit apertures in lumen of vessel element. 21. *E. zuluensis (Van Wyk, 2662)* showing vestures in and around pit apertures in lumen of vessel element. 22. *E. zeyheri* — note heterogeneous rays and overlapping tails of vessel elements (A). 23. *E. zeyheri*, tangential section of procumbent ray cells. 24. Radial section of *E. zeyheri* (all *Van Wyk, 3189*), upright ray cells — note slightly disjunctive cell walls. Scale line = 5 μm (Figures 19 – 21, 23 & 24) or 50 μm (Figure 22).

(Dadswell & Eckersley 1935; Stern 1954) or vertical concentric canals of the lysigenous type (Ingle & Dadswell 1953). Gum veins have been reported in Myrtaceae in the wood of *Angophora* Cav., *Eucalyptus* L'Hérit., *Spermolepis* Brogn. & Gris. (all Leptospermoideae) and *Rhodamnia* Jack of the Myrtoideae (Record 1918, 1925 & 1936; Ingle & Dadswell 1953; Dadswell 1972). It is apparently absent in *Eugenia* from the New World (Record & Hess 1949) and South-West Pacific area (Ingle & Dadswell 1953).

In southern African species of *Eugenia* the parenchyma strands in which the gum is deposited are without doubt identical to pith flecks (Brown 1913). Pith flecks are confined to hardwoods and are commonly caused by the larvae of cambium miners belonging to the insect genus *Phytolobia* (Panshin & De Zeeuw 1980). Stone (1921) reported pith flecks in the wood of *E. mespilioides* Lam.

In the investigated *Eugenia* spp. the pith flecks (Figures 25 & 26) are usually limited to the early wood of a growth ring and appear to be initiated by the vascular cambium at the onset of cambial activity in spring. This corresponds with the fact that *Phytolobia* infestation usually occurs in early spring (Record 1911; Brown 1913). Thus in transverse section the inner borders of the strands are usually straight and the outer convex. Each pith fleck consists largely of more or less isodiametric parenchyma cells either arranged in weak radial tiers or without definite patterns (Figures 25 & 27). Most of these cells are tanniniferous with abundant starch grains. Brachysclereids, large fibres and parenchyma cells without tanniniferous contents are occasionally present (Figure 30). In general appearance, these parenchyma cells resemble more closely the upright cells of the rays than the axial parenchyma cells. Radial sections clearly show a continuation between the parenchyma of the pith flecks and rays (Figure 28).

Amorphous material (blue, yellowish- or greenish-brown in stained sections) is usually deposited intercellularly, mainly in tangential bands within the central portion of a pith fleck or at the interface between the parenchyma strand and the previous season's late wood (Figure 27). Deposits have been observed in most pith flecks and the process appears to be lysigenous.

Vertical strands of crystalliferous cells (apparently homologous to the chambered crystalliferous strands of the axial parenchyma, see 3.2(f)) are frequently associated with the parenchyma of pith flecks (Figure 28). Each cell (chamber) contains a single prismatic crystal differing from those of the axial parenchyma in that it is smaller and lacks a thick lignified sheath surrounding the crystal (Figure 29). In addition the sides of these crystals often appear slightly concave under the light microscope in comparison to the straight sides of those in axial parenchyma. Pith flecks with several radial tiers of crystalliferous cells (and without gum) are occasionally present (Figure 26).

The crystals associated with the pith flecks are identical in shape and size to those in the phloem. Fibres associated with these radial tiers of crystalliferous cells are also similar to those in the bark. Indications are that these cells (Figures 26 & 30) developed from undifferentiated phloem cells enclosed in the xylem following the formation of a cambium bridge on the phloem side of the damaged cambium (the formation of pith flecks is discussed in detail by Record (1911) and Brown (1913)).

In southern African species of *Eugenia*, pith flecks and/or gum veins are sporadically present in wood samples from all species. They are abundant in *E. simii, E. verdoorniae* and *E. umtamvunensis*, but rare in *E. zeyheri* and *Eugenia* sp. A. This oculd be significant as in other morphological features *Eugenia* sp. A. seems to be most closely related to *E. zeyheri*.

The mere presence or absence of gum veins must be cautiously used as a diagnostic characteristic because of its reported traumatic origin. It may consequently be absent from a particular specimen. However, Record (1918, 1925 & 1936) has found that the presence of axial and also radial canals in wood is a valuable diagnostic feature.

According to Jane (1970) little is known about the origin of traumatic axial canals. Natural causative factors for gum vein formation in *Eucalyptus* include bark (cambium) damage by fire, insects, branch shedding and accidental mechanical injury (Jacobs 1937). For references to authors claiming other factors see Hillis & Brown (1978). However, the cause of gum veins (strictly speaking pith flecks) in *Eugenia* is unknown. With the exception of species growing on the forest edge, fire can be ruled out as a factor in wood collected from inside well protected forests. Most of the wood samples examined have never been exposed to fire. Being a riverine species, *E. simii* is frequently subjected to mechanical injury during floods. This may account for the abundant gum veins in this species. Considering that the gum veins in *Eugenia* develop in pith flecks, it is assumed that insect activity could be the main factor.

It is necessary to consider the relationship between gum veins and pith flecks. According to Brown (1913) gummosis of pith flecks was probably first noted as early as 1863 by Wiegand in the wood of *Prunus avium* L. Brown's own observations confirmed that pith flecks are the starting point for gum formation in a number of *Prunus* species. Record (1918) also noted pith flecks with axial intercellular canals in members of the Rutaceae. *Prunus* has often been listed as an example of a genus that may have gum veins (e.g. Record 1936; Panshin & De Zeeuw 1980; IAWA Committee 1981). However, no mention is made of the connection between pith flecks and gum veins in the glossaries of wood terms by, among others, the IAWA Committee (1964) and Ford-Robertson (1971).

We are convinced that gum veins and pith flecks are homologous in southern African species of *Eugenia*. Pith flecks gradually change into gum veins following gummosis of some parenchyma cells. A somewhat similar, although more complex series of events is involved in the development of kino veins in *Eucalyptus obliqua* L'Hérit. (Skene 1965).

Record (1911) and Brown (1913) were among the first to point out that pith flecks are clearly of pathological origin and therefore of no taxonomic value. However, the potential of pith flecks to undergo gummosis may be taxonomically significant. Indications are that differences in the structure of gum veins may be taxonomically important in Myrtaceae — especially at supraspecific levels. No comparative study on this feature is available at present.

(f) *Crystals*

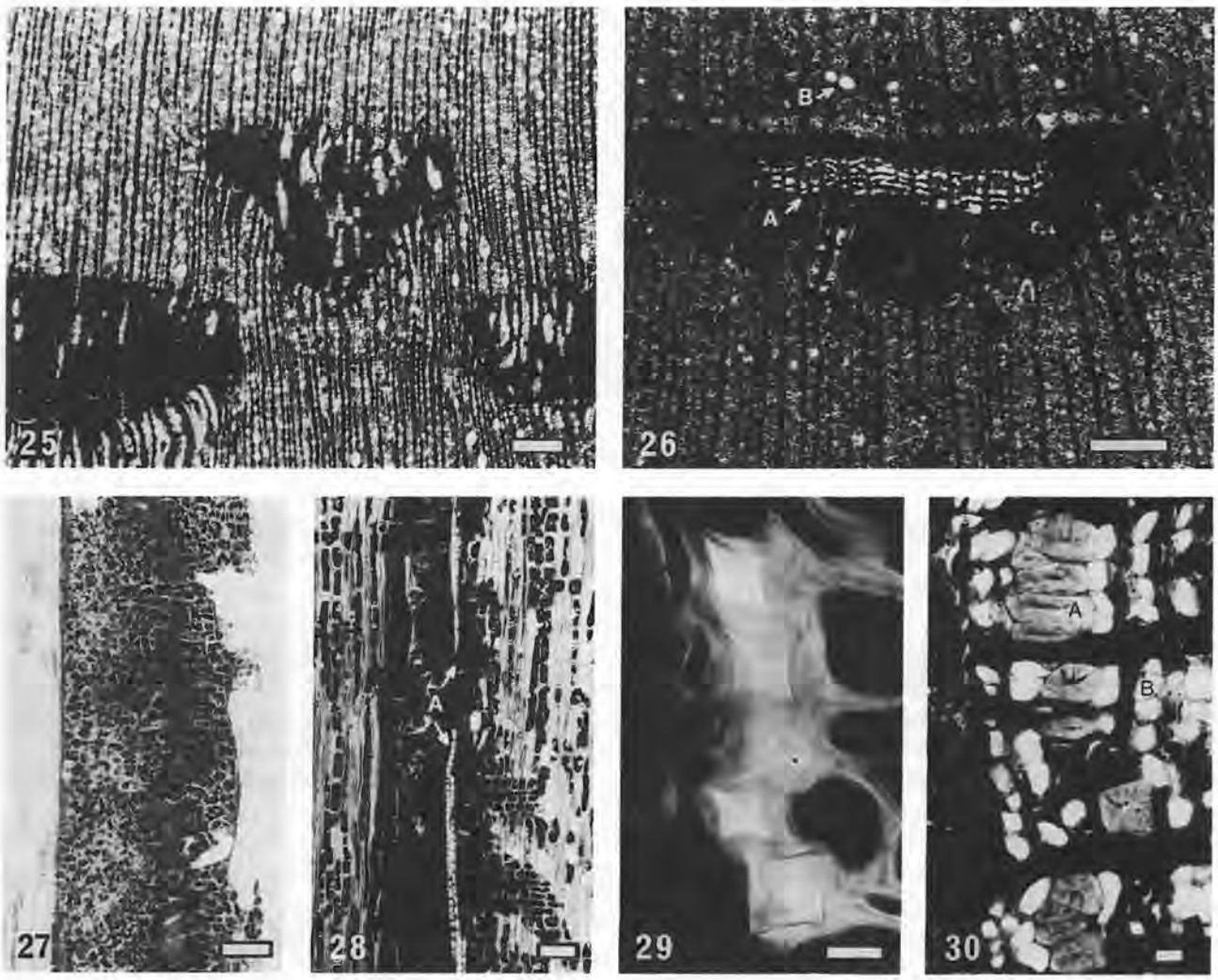
Prismatic crystals of, presumably, calcium oxalate occur in the wood of all *Eugenia* specimens examined. According to Chattaway (1955, 1956) this is the most common of all crystal types in wood. It has been recorded in wood from *Eugenia* species as well as from other members of the Myrtaceae (Solereder 1908; Metcalfe & Chalk 1950; Ingle & Dadswell 1953; Chattaway 1955, 1956).

Crystalliferous cells are restricted to the axial parenchyma and parenchyma associated with pith flecks. Crystals from the latter tissue differ from those in the axial parenchyma and have already been dealt with (see 3.2(e)). In southern African species of *Eugenia* Van Wyk (1978) recorded prismatic crystals in the secondary xylem and phloem of twigs and leaves. Druse crystals are present in the cortex, pith and mesophyll. These observations suggest that the presence of a particular type of crystal is correlated with the type of tissue in which it occurs. This phenomenon was also observed in the Icacinaceae and might be of taxonomic value in distinguishing between higher taxa (Heintzelman & Howard 1948).

The relative abundance of the crystals shows considerable variability between specimens as well as within a sample of wood. There is a definite tendency for the crystalliferous cells to be associated with the late wood of certain growth rings (Figure 31). Crystals are also characteristic for the late wood of *Robinia pseudo-acacia* L. (Czaninski 1968) and *Daniellia oliveri* (Rolfe) Hutch. & Dalz. (Amobi 1974).

Crystals occur solitary in usually chambered cells (Figures 32 & 33) and sporadically in undivided axial parenchyma cells (Figures 35, 36 & 39). Only one cell with more than one prismatic crystal has been observed. Crystalliferous cells or chambers are usually isodiametric or axially elongated. Strands with radially elongated cells are occasionally present in some specimens (Figures 38 & 41). Cell walls are usually lignified and thicker than those of normal axial parenchyma cells. Single, comparatively larger crystalliferous cells (idioblasts), often with richly pitted cell walls, do occur but are infrequent (Figure 39).

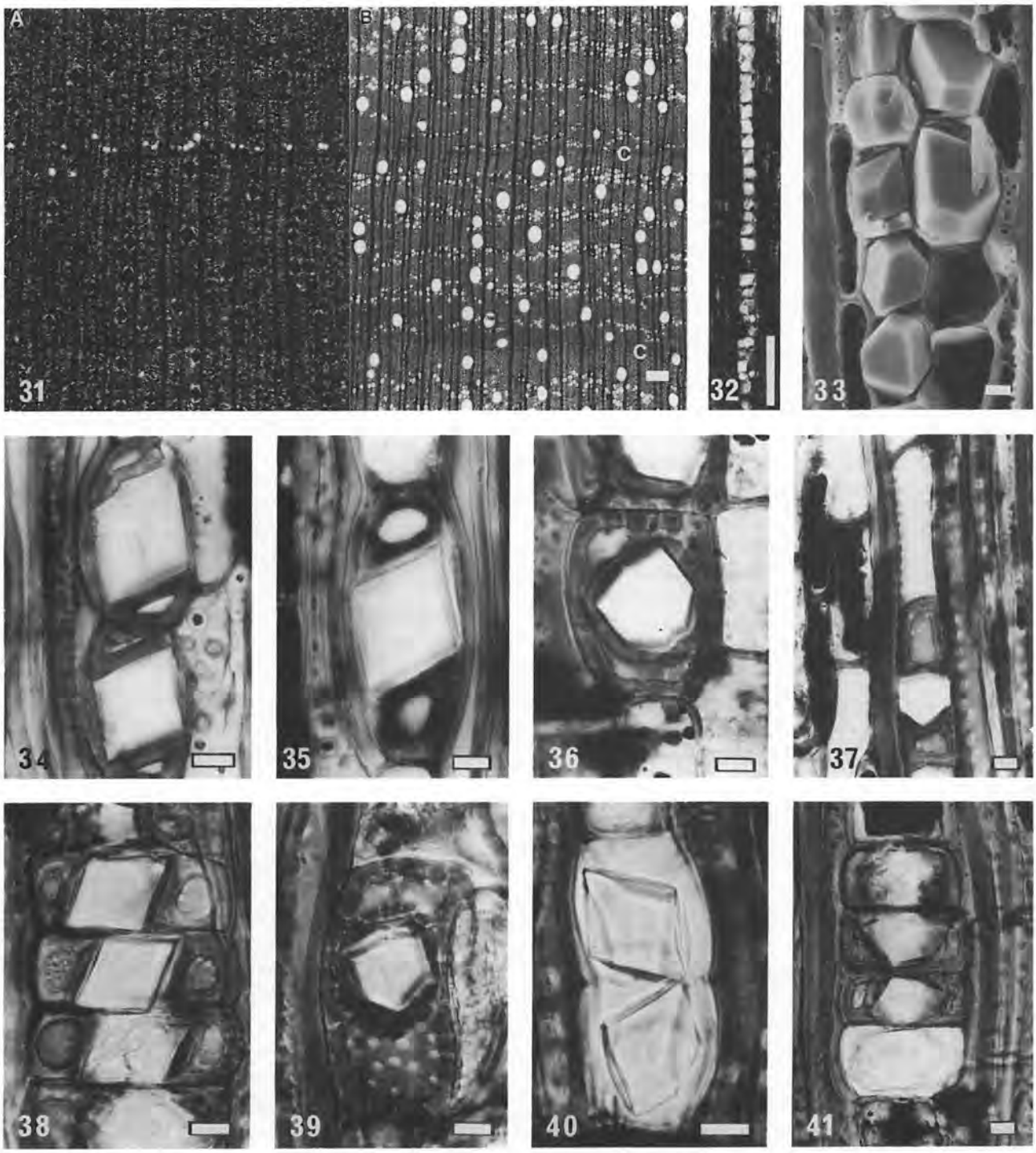
A chambered cell has been defined as a crystalliferous cell divided into compartments by septa (IAWA Committee 1964). In *Eugenia* these chambers are often separated



Figures 25 – 30 Morphology of pith flecks (gum veins). 25. Transverse section of *Eugenia simii (Van Wyk, 2519)* showing pith flecks and very little gummosis. 26. Transverse section of *E. simii (Van Wyk, 4520)* showing a pith fleck with abundant crystalliferous cells (A) under polarized light. Compare size of these crystals with those in axial parenchyma (B). 27. Radial section of *E. zuluensis (Van Wyk, 2662)* showing a gum vein with gum deposits. Note abundant starch grains in associated parenchyma cells. 28. Radial section of *E. verdoorniae (Van Wyk, 1696)* showing crystalliferous strands (A) in gum vein. 29. Transverse section of *E. capensis (Van Wyk, 2586)* showing prismatic crystals in gum vein — note slightly concave facets of crystals. 30. Transverse section of *E. simii (Van Wyk, 4520)* showing thick-walled sclereid-like fibres (A) in parenchyma of a pith fleck — note crystalliferous cells (B). Scale line = 200 μm (Figures 25 – 28) or 20 μm (Figures 29 & 30).

during maceration. This separation could be explained either by assuming that the primary septa dividing the original cell remain unlignified and are dissolved during maceration (as has in fact been reported by Bridgwater & Baas (1978) for the Punicaceae), or by the fact that the strands develop by the repeated division of fusiform derivates to produce axial files of small cells. If the latter applies, the use of 'chambered cell' in descriptions does not comply with the IAWA definition.

Almost all crystals are surrounded by a lignified sheath. This sheath is particularly well developed on those facets of the crystal not in direct contact with the cell wall (Figures 34 – 39). It appears to be identical in composition to the lignified cell wall with which it is often continuous. The



Figures 31 – 41 Morphology of prismatic crystals. 31A & B. Transverse section of *Eugenia erythrophylla (Van Wyk, 3342)* showing crystals (A, polarized light) associated with one of two bands of late wood (C). 32. Tangential section of *E. zeyheri (Van Wyk, 3134)* showing crystalliferous chain under polarized light. 33. SEM micrograph of *E. umtamvunensis (Van Wyk, 4232)* showing chambered crystalliferous cells. 34. Radial section of *E. capensis (Van Wyk, 4508)* showing two crystalliferous chambers. 35. Radial section of *E. capensis (Van Wyk, 2586)* showing a crystalliferous axial parenchyma cell. 36. Radial section of *E. simii (Van Wyk, 1270)* showing a crystalliferous chamber — note pit in sheath surrounding the crystal. 37. Radial section of *E. woodii (Van Wyk, 2805)* showing a crystalliferous and normal axial parenchyma cell. 38. Radial section of *E. zeyheri (Van Wyk, 3126)* showing a crystalliferous strand with radially elongated chambers. 39. Radial section of *E. woodii (Van Wyk, 2973)* showing a crystal idioblast. 40. Radial section of *E. zeyheri (Van Wyk, 3126)* showing two chambers with crystals not enclosed by a thick lignified sheath. 41. Radial section of *E. simii (Van Wyk, 4243/2)* showing bottom chamber of crystalliferous strand with crystal not enclosed by a lignified sheath. Scale line = 100 μm (Figures 31 & 32) or 10 μm (Figures 33 – 41).

presence of this sheath suggests that it might be a means of isolating the crystal which is often regarded as an excretory and toxic end product of metabolism. However, this is probably not a complete isolation because the cell wall and sheath usually contain pits (Figures 36 & 39). Furthermore, a few crystals with thin, unlignified sheaths are sometimes present, either as separate strands or as single cells scattered within a strand of cells with lignified sheaths (Figures 40 & 41).

Crystals surrounded by a sheath which appears to be composed of cellulose are fairly widespread in plants (Hirata *et al.* 1972; Butterfield & Meylan 1980; Franceschi & Horner 1980). Haberlandt (1914) reported the occasional lignification or suberization of this cellulose sheath. Frank & Jensen (1970) showed that prismatic calcium oxalate crystals in the leaves of *Canavalia ensiformis* DC. each originate in a vacuole and are delimited by a membrane which thickens by the deposition of wall material probably including cellulose and lignin. Chattaway (1953) briefly refers to the formation of thick walls around calcium oxalate crystals in such a way as to create the impression that it is a widespread occurrence in plants. However, crystals enclosed in a thickened sheath of lignified cell wall material have rarely been reported as such in anatomical wood descriptions. Czaninski (1968) described such a sheath from prismatic crystals in the axial parenchyma of *Robinia pseudo-acacia*. Illustrations of crystalliferous cells rather similar to those in *Eugenia* have occasionally been observed in the literature, for example in *Pterocarpus soyauxii* Taub. (Brazier & Franklin 1961, plate 29-B), *Leptospermum ericoides* A. Rich. (Ingle & Dadswell 1953, plate 9:6) and *Juglans nigra* L. (Panshin & De Zeeuw 1980, Figure 5.12A).

Although starch grains frequently occur in tanniniferous parenchyma cells, they have never been observed within crystalliferous cells. Our observations also confirm the comment by Scurfield *et al.* (1973) that crystals and polyphenols (tannins) appear to be mutually exclusive.

The shape and location of calcium oxalate crystals in plants are often very specific and have occasionally been used in classifications (for references see Franceschi & Horner 1980). Crystals are also often useful as diagnostic features in wood identification (Metcalfe & Chalk 1950; Chattaway 1955, 1956; Dadswell 1972). Despite the widespread occurrence of prismatic crystals in plants, the patterns of wall thickening in crystalliferous cells are often sufficiently discontinuous and consistent to be useful as diagnostic features at mainly family and sometimes generic level (Solereder 1908; Metcalfe & Chalk 1950; Chattaway 1956). It appears, however, as if the potential taxonomic value of the sack or sheath surrounding crystals has hitherto not received serious attention. As far as we have ascertained, crystals with thickened sheaths resembling those in the southern African *Eugenia* species have not previously been reported for this genus. There is, however, the possibility that this feature could have been overlooked or treated as trivial. We are thus not in a position to evaluate the taxonomic significance of the encysted crystals in the southern African *Eugenia* species. Although no interspecific differences in crystal features were found in this study, these features could still be diagnostic at generic or higher levels.

(g) *Vestured pits*

Vestures occur in the bordered pits of all the wood samples examined. This is characteristic for the Myrtaceae and most of the other families assigned to the Myrtales (Bailey 1933; Metcalfe & Chalk 1950).

As a result of the pores being solitary, intervascular pits are limited to the overlapping tails of vessel elements. In addition, vessel walls have a collection of vessel-fibre, vessel-ray and vessel-parenchyma pits. It was difficult and frequently impossible to distinguish between these pit types when examining the surface of a vessel element with the SEM.

Most vessel pits are vestured to some degree although unvestured ones are occasionally present. Simple pits of half-bordered pit pairs always lack vesturing (Figure 42). Vestures are also absent from the simple pit areas sometimes present in vessel members.

The appearance of the vestures when viewed from the pit floor into the pit chamber shows great variation between wood samples, different vessel elements within a sample and sometimes in a single vessel element. The latter variation could be ascribed to the different cell types which abut on the vessel elements. Some of the observed variation is shown in Figures 43 – 50.

Most of the vestures are attached to those areas of the roof of the pit chamber which are near the pit canal. From the pit floor the vestures appear as a closed to open mat of coarse or fine branch-endings, branched and anastomosing filaments or stout, often hardly branched protuberances. Towards the pit floor the vesturing often grades into a few scattered bead-like papillae. The lowest part of the pit chamber roof is usually devoid of vestures. According to Van Vliet (1978) this marginal zone could result from the lack of space in the corner between pit roof and pit floor.

Vestures also occur infrequently in and around the pit apertures. It may even spread beyond the pit aperture onto the surrounding lumen surface of the vessel wall and sometimes completely obscure the pits (Figures 20 & 21). However, the degree of pit aperture vesturization can vary considerably in the lumen of a vessel element.

In the same sample, the bordered pit chambers of fibre tracheids are usually conspicuously less vestured than those of vessel elements (Figures 11 & 12). Again considerable variation in vesture morphology between and within samples was observed. Vestures are usually absent from the slit-like pit apertures.

Following the scheme of Van Vliet (1978) most of the vestures in the vessel pits of southern African species of *Eugenia* can be classified as Type B form 1, 2 and 3. Van Vliet (1978) also recorded this type in Myrtaceae. However, owing to the many intermediate forms, we agree with Butterfield & Meylan (1980) that no scheme for classifying vestures into morphological types so far proposed, is entirely acceptable.

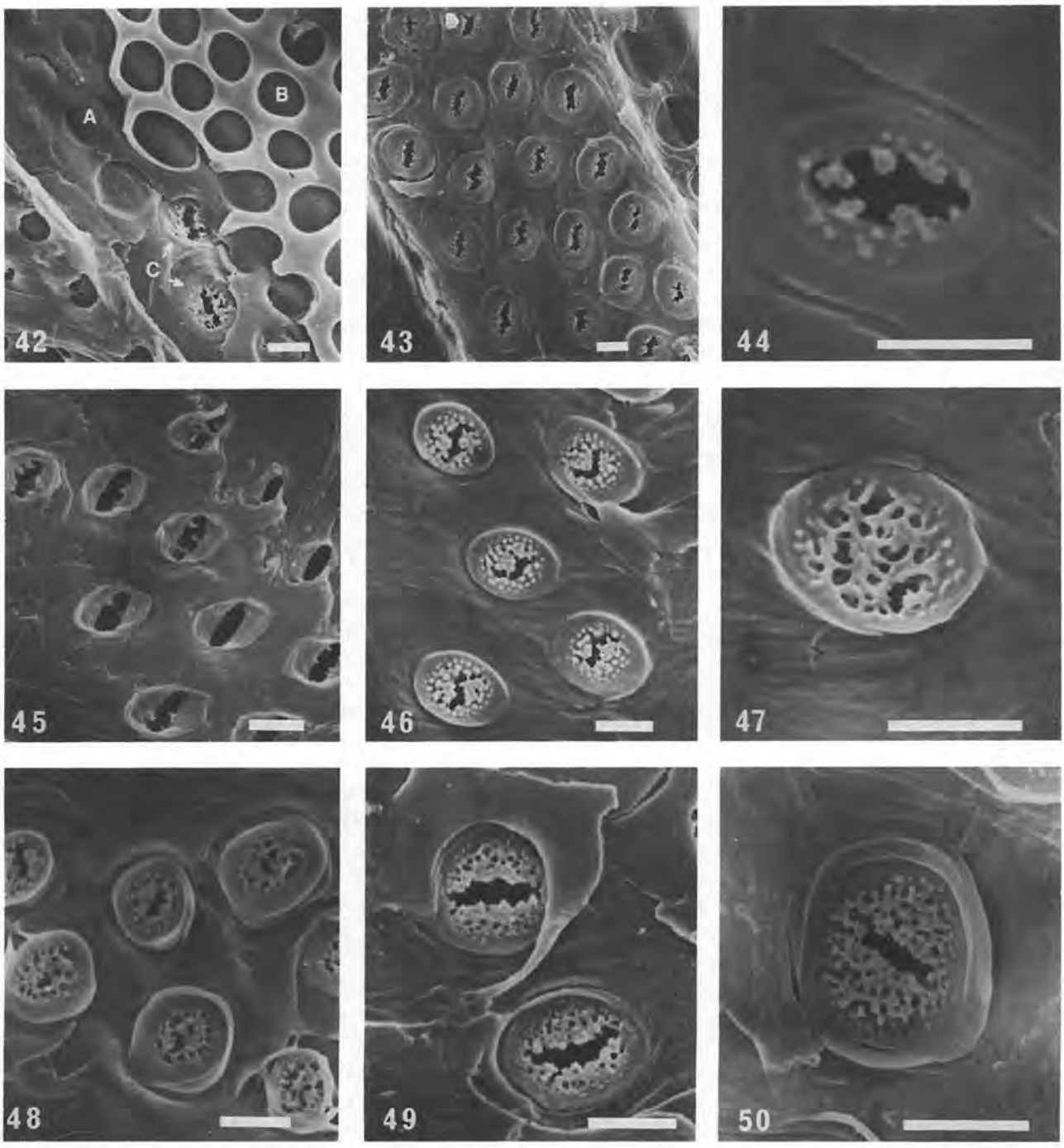
Efforts to apply the morphology of the vestured pits of southern African species of *Eugenia* diagnostically at the species level proved to be futile. We could also find no support from this source for the proposed supraspecific grouping of the species.

(h) *Miscellaneous features*

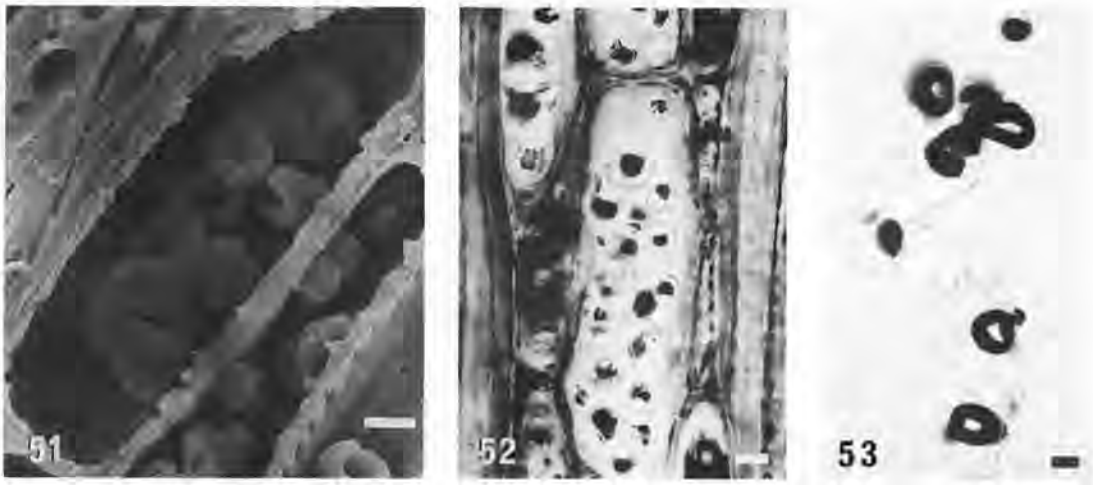
Starch grains in the wood of southern African species of *Eugenia* are usually simple or 2(3)-compound, more or less spherical, but angular when crowded. In permanently mounted wood sections the hollow centres (hilums?) often appear as dark-coloured spots under the light microscope (Figure 52). This may be the optical effect of air trapped within the grain. The use of steam during sectioning may contribute towards this phenomenon because we did not observe these dark markings in freehand wood sections mounted in glycerine. Thin sections of starch grains clearly revealed that they are usually hollow (Figure 53). In SEM preparations grains are often collapsed with concave sides (Figure 51).

Many authors, notably Reichert (1913), have convincingly shown that valuable taxonomic criteria may be derived from a careful study of starch grains. However, there is a strong possibility that the observed hollow centres could be artefacts caused by swelling of the starch grains (Badenhuizen 1959). Unfortunately we did not have adequate data on the morphology of starch grains in Myrtaceae for comparative purposes.

Record & Hess (1949) reported a visual distinction between the heartwood and sapwood of *Eugenia* from the



Figures 42 – 50 SEM micrographs to show the morphology of vestured pits in vessel elements. 42. *Eugenia umtamvunensis (Van Wyk, 3631)* showing vessel-parenchyma pitting with intact pit membranes (A), lack of vestures in simple pits of half-bordered pit pairs (B) and vestured pit chambers (C) in vessel wall. 43. *E.* sp. B (*Van Wyk, 2629*). 44. *E. simii (Van Wyk, 1269)*. 45. *E.* sp. B (*Van Wyk, 2629*). 46. *E. umtamvunensis (Van Wyk, 3631)*. 47. *E. natalitia (Van Wyk, 4252)*. 48. *E.* sp. A (*Van Wyk, 2630*). 49. *E. zuluensis (Van Wyk, 2662)*. 50. *E. woodii (Van Wyk, 2973)*. Scale line = 2,5 μm.



Figures 51 – 53 Morphology of starch grains. 51. SEM micrograph of *E. woodii (Van Wyk, 2973)* showing axial parenchyma cells with starch grains — note collapsed appearance of grains. Tangential section of *E. erythrophylla (Van Wyk, 1698)* showing axial parenchyma cells with dark-centred starch grains. 53. Thin-sectioned starch grains of *E. natalitia (Van Wyk, 4254)* showing the hollow centres — stained with IK1. Scale line = 5 μm.

New World. No such distinction could be made in the wood of the southern African species. A visual distinction between heartwood and sapwood appears to be the exception rather than the rule in a number of *Eugenia s. l.* species from the Old World (Reyes 1938; Desch 1954). Unfortunately Ingle & Dadswell (1953) did not give information on this aspect. This feature may be present in old trees with thick boles. The maximum diameter of stems used in this study did not exceed 0,2 m.

Wood of species from Group X tends to be pinkish-brown and that of species from Group Y yellowish-brown. However, many exceptions occur and this feature is of no diagnostic value.

Basic specific gravity (specific gravity converted at 6% moisture content) as well as the burning splinter test proved to be of no interspecific taxonomic value.

3.3 Generic delimitation of *Eugenia* in southern Africa

Two genera of the Myrtoideae, viz. *Eugenia* and *Syzygium* are at present being recognized in southern Africa. In his revision of *Eugenia* in southern Africa, Dümmer (1912) included *Syzygium* under *Eugenia*. He obviously followed the wide generic concept of Bentham & Hooker (1862 – 67) who treated *Eugenia* as a collective genus including many species from the tropical and subtropical parts of both the New and Old World. Bentham & Hooker reduced more than 40 genera to *Eugenia s. l.* According to Schmid (1972a) there are about 70 synonyms for this inclusive genus.

However, several subsequent workers (see Schmid 1972a for a detailed discussion and references) advocated the acceptance of a number of segregate genera. Foremost among these authors were E.D. Merril and L.M. Perry who segregated the large Old World genus *Syzygium* from *Eugenia s. l.* They also reinstated a number of small Old World genera including the somewhat vaguely circumscribed *Jossinia* Comm. ex DC. *Jossinia* includes a few Old World species showing close affinity to some American species of *Eugenia* (Diels 1922; Merril 1950a & b). *Eugenia s. str.* in the sense of Merril & Perry retains the species from the New World only.

Although no southern African species of *Eugenia* have been placed in *Jossinia*, Merril (1950a & b) would probably have included these species in this segregate genus. However, various subsequent workers considered *Jossinia* congeneric with *Eugenia s. str.* — thereby recognizing members of *Eugenia s. str.* from the Old World, including Africa (e.g. Amshoff 1958; Schmid 1972b; Van Wyk 1978; White 1977 & 1978; Briggs & Johnson 1979; Scott 1979).

In his paper on the floral morphology of *Eugenia*, Schmid (1972b) says: 'All evidence from both vegetative and reproductive organography and anatomy now available (see Schmid 1971) demonstrates that *Jossinia* is so very similar to the American species of *Eugenia s. str.* that segregation of *Jossinia* as a genus seems unwarranted'. He concludes that *Jossinia* may represent a residue of Old World species of *Eugenia s. str.* Some of its taxa exhibit rather primitive floral anatomical features, perhaps transitional between the Old World *Syzygium s. l.* and the New World *Eugenia s. str.* Our results on wood anatomy lend some support to this view.

Comparative anatomical studies of wood (Dadswell & Ingle 1947; Ingle & Dadswell 1953; Chattaway 1959) support a distinction between the mainly New World *Eugenia s. str.* (including the Old World *Jossinia*) and the Old World *Syzygium s. l.* This division is also supported by several other comparative morphological studies (see Schmid 1972a for a discussion). In their comprehensive study, Ingle & Dadswell (1953) found no evidence to distinguish between *Eugenia s. str.* from the Old World (?*Jossinia* sensu Merril) and the New World. Neither could they find support for the segregation of *Acmena* DC. and *Cleistocalyx* Blume from *Syzygium s. l.* In Table 2 the most significant anatomical differences between the two groups mentioned above and the wood features of the southern African species of *Eugenia s. str.* are compared.

The wood anatomical descriptions of southern African species of *Syzygium* by Kromhout (1975; 1977) conform to the characteristics for this taxon (Table 2). It therefore supports the separate status of *Syzygium* and *Eugenia* in southern Africa — a distinction also supported by other morphological features (Van Wyk 1978). From Table 2 it

Table 2 Selected wood features: southern African species of *Eugenia s. str.* compared with *Syzygium s. str.* and *Eugenia s. str.* from other parts of the world

Anatomical features	Old and New World species of *Eugenia s. str.*: excluding southern African species[a]	*Syzygium s. str.*[b]	Southern African species of *Eugenia s. str.*
Vessels	Small[c] (average maximum tangential diameter 75 – 90 μm), solitary.	Small to moderately large (average maximum tangential diameter 97 – 206 μm), mainly in short radial multiples or clusters.	Small (average maximum tangential diameter 50 – 90 μm), solitary.
Vessel pitting	Small (diameter of pit borders 4 – 5 μm).	Medium-sized (diameter of pit borders 8 – 12 μm).	Small (diameter of pit borders 3 – 6 μm).
Ray-vessel pitting	Small, half-bordered and similar to vessel type.	Half-bordered, but apparently simple, rounded to elongated, either oblique or in scalariform arrangement, sometimes unilaterally compound.	Small, half-bordered and similar to vessel type.
Ray cells	Upright cells frequently disjunctive.	Disjunctive upright cells apparently not observed.	Upright cells frequently disjunctive.
Vasicentric tracheids	Present.	Absent.	Present although very sparse and occasionally apparently absent in some samples.
Parenchyma	Apotracheal.	Paratracheal.	Apotracheal.
Fibre pitting	Numerous, distinctly bordered.	Pits inconspicuous and indistinctly bordered.	Numerous, distinctly bordered.
Gum veins	Not reported.	Not reported.	Occasionally present — developing from pith flecks.
Heartwood/ sapwood	Visually distinguishable (Old World?)	With or without visual distinction.	No visual distinction.

[a]From Dadswell & Ingle (1947), Record & Hess (1949) & Ingle & Dadswell (1953).
[b]From Dadswell & Ingle (1947), Ingle & Dadswell (1953) & Desch (1954).
[c]Size classes follow Chattaway (1932).

seems that anatomically, the southern African species of *Eugenia s. str.* show close affinity to this genus in the New World and other parts of the Old World. Anatomical features recorded in *Eugenia* from southern Africa only, are the occasional presence of gum veins and the lack of a clear colour distinction between heartwood and sapwood (more information on the latter feature is required for *Eugenia s. str.* from the Old World). Furthermore vasicentric tracheids are sparse in the southern African species and appear to be absent in some samples.

Polygamy (to mention but one non-anatomical feature) is characteristic for *Eugenia* in southern Africa (and probably the rest of Africa). Plants are androdioecious and only very rarely andromonoecious . This phenomenon is very rare in Myrtoideae (Schmid 1980) and apparently absent in *Eugenia* from at least the New World and South-West Pacific area.

Pending further study, we shall tentatively treat *Eugenia* in southern Africa as congeneric with the mainly American *Eugenia s. str.* However, it is evident from the discussion above that aspects of the generic relationship of the southern African *Eugenia* species are still unsettled. In addition *Eugenia* in southern Africa comprises two supraspecific groups of unknown status (Van Wyk *et al.* 1980; Van Wyk 1980; Van Wyk *et al.* 1982). The relationship of this heterogeneous taxon with the American eugenioid genera (McVaugh 1968) or with the *Eugenia* alliance of Briggs & Johnson (1979), is still unclear. The main obstacle is the paucity of published data that can be used for comparative purposes.

4. Conclusions

The wood anatomy of the southern African species of *Eugenia* agrees with the general wood anatomical descriptions for Myrtaceae.

Eugenia in southern Africa is anatomically quite distinct from *Syzygium*. This supports the proposed division of *Eugenia s. l.* into at least *Eugenia s. str.* and *Syzygium s.l.*

The wood anatomy of southern African species of *Eugenia* largely resembles that of *Eugenia s. str.* in other parts of the Old World as well as in the New World. However, features only present in the southern African species include the occasional absence of vasicentric tracheids, the presence of gum veins in some specimens and no visual distinction between heartwood and sapwood.

No single characteristic or combination of characteristics could be found to be diagnostic at the species level. Features that might be useful to distinguish between some species are the average tangential pore diameter (only in species with extreme values) and the lack of tannin in the ray cells.

The wood anatomy rendered no support for the proposed division of the native species of *Eugenia* into two supraspecific groups.

The taxonomic significance of a number of structural features could not be evaluated owing to the paucity of comparative information. These are the structure of the gum veins, crystals enclosed by a thick lignified sheath and hollow starch grains.

Although *Eugenia s. str.* is upheld in southern Africa at present, there are a few characteristics which cast some doubt on its generic identity. There is a need for a detailed

organographical and anatomical comparison with the 'eugenioid' genera in other parts of the world.

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CHAPTER 6

STRUCTURE AND TAXONOMIC VALUE OF THE FIRST-FORMED STEM PERIDERM

Jl S. Afr. Bot. 46 (1): 67–88 (1980)

THE GENUS *EUGENIA* L. (MYRTACEAE) IN SOUTHERN AFRICA: 1. THE NATURE AND TAXONOMIC VALUE OF THE FIRST-FORMED STEM PERIDERM*

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ABSTRACT

The nature of the first-formed stem periderm of some *Eugenia* species of Southern Africa was examined. Both the quantitative and qualitative characteristics of this tissue were evaluated for their taxonomic importance. This was done on the basis of a review of the known taxonomic value of the periderm with special reference to its application in the Myrtaceae.

A number of periderm characteristics were found which support the division of the species into two distinct groups. The most important of these is the position in which the periderm originates in the stem. From this it can be concluded that the first-formed stem periderm initiates either in the cortex (Group X) or in the primary external phloem (Group Y). This characteristic is correlated with two structurally different types of phellem and proves to be constant for a species. The identity of species with a hitherto vague taxonomic position, could be ascertained by checking the position in which the periderm originates in the type specimens.

The grouping of specimens based on periderm characteristics, closely agrees with the revision of Dümmer (1912). It does, however, not support the delimitation of some of the taxa as proposed by White (1977) in the most recent revision of the genus *Eugenia* in Southern Africa.

UITTREKSEL

DIE GENUS *EUGENIA* L. (MYRTACEAE) IN SUIDELIKE AFRIKA:
1. DIE AARD EN TAKSONOMIESE BETEKENIS VAN DIE EERSTE GEVORMDE STINGELPERIDERM

Die aard van die eerste gevormde stingelperiderm van 'n aantal *Eugenia*-spesies uit Suidelike Afrika is ondersoek. Beide kwantitatiewe en kwalitatiewe kenmerke van hierdie weefsel is vir hul taksonomiese waarde geëvalueer. Dit is gedoen in die lig van 'n oorsig van die reeds bekende taksonomiese waarde van die periderm met besondere verwysing na die toepassing daarvan in die Myrtaceae.

'n Aantal peridermkenmerke wat die verdeling van die spesies in twee verskillende groepe ondersteun, is gevind. Die belangrikste hiervan is die posisie in die stingel waar die

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periderm ontstaan. Hiervolgens kan die eerste gevormde stingelperiderm òf in die korteks (Groep X) òf in die primêre eksterne floëem (Groep Y) ontstaan. Hierdie kenmerk is met twee struktureel-verskillende tipes felleem gekorreleer en blyk konstant te wees vir 'n spesie.

Deur die posisie van peridermvorming by die tipe-eksemplare te kontroleer, kon die identiteit van spesies waarvan die taksonomiese posisie tot nog toe vaag was, vasgestel word.

Daar is gevind dat die groepering van eksemplare volgens peridermkenmerke nou ooreenstem met die hersiening van Dümmer (1912), maar nie die omgrensing van sommige taksons soos voorgestel in die jongste hersiening van die genus *Eugenia* in Suidelike Afrika (White, 1977), ondersteun nie.

1. Introduction

The genus *Eugenia* L. is one of the largest woody genera in the world (Good, 1969) and taxonomically one of the most difficult taxa to deal with. There are few other genera that confront the taxonomist with so many problems. One of these is the lack of useful and reliable external morphological characteristics which may be used to distinguish between the hundreds of described species.

This is also the case with the *Eugenia* species of Southern Africa where many herbarium specimens cannot be identified.

As an introduction to a revision of *Eugenia* in Southern Africa, an anatomical study of the leaf and stem has been undertaken (Van Wyk, 1978). One of the objectives was to evaluate a number of anatomical characteristics as an aid to the identification of taxa and to use such diagnostic characteristics to determine the identity of hitherto vaguely known species. It is the aim of this paper to describe and evaluate some characteristics of the first-formed periderm in the stem, and to discuss some of its taxonomic implications. Before evaluating the periderm characteristics it is necessary to briefly review the known taxonomic value of this tissue with special reference to its application in the Myrtaceae.

In comparative anatomical studies characteristics of the bark or rhytidome rather than only those of the periderm, are usually used. Despite the diagnostic appearance of the external surface pattern of the bark of many woody plants, not much effort has been made to correlate it with the internal structure (Whitmore, 1962 (a), (b) and (c)). The work of Douliot (1889) according to Carlquist (1961) nevertheless already contains systematically arranged information on the site of periderm initiation for a large number of genera. In a revision of the genus *Eugenia* s.l. in Malaya, Henderson (1949) stressed the large diagnostic value that the bark of this genus possess in field studies.

According to Lignier (1887, 1890) the phellem of the Myrtaceae consists of layers of radially flattened cells with thin or sclerified walls alternating with radially elongated thin-walled cells. The cell walls of the radially flattened cells are not suberised and are known as phelloids (Esau, 1965). Van Tieghem (1904) according to Solereder (1908) showed that the cell-shape of the different layers can also be the reverse of Lignier's results. Phellem consisting only of cubical thin-

walled cells occurs in some species of *Eucalyptus* and *Syzygium* (Metcalfe & Chalk, 1965).

The first-formed periderm in the stem of the Myrtaceae usually either originates in the parenchyma cells of the cortex or in the primary external phloem to the inside of the extraxylery ring of fibres (Blyth, 1958)—also called the pericycle (Lignier, 1887; Metcalfe & Chalk, 1965). According to Lignier (1887) the method of decortification is one of the more constant stem characteristics of the Myrtaceae that can be used for the purpose of identification. Although this characteristic is of value for the recognition of genera and subgenera (Solereder, 1908) it is important to bear in mind that the first-formed periderm is always more superficial than successive periderms (Metcalfe & Chalk, 1965). Metcalfe and Chalk (1965) also question the taxonomic value of the exact position in which the periderm originates (e.g. superficial or deep in the cortex). For the genus *Eugenia* the position in which the periderm originates can vary according to the species (Metcalfe & Chalk, 1965).

As examples of bark studies in the Myrtaceae the works of Brögli (1926) on *Eucalyptus* and *Eugenia* and Chattaway (1955 (a), (b), (c), 1959) on *Eucalyptus*, deserve mentioning. Chattaway (1953) found that the first-formed periderm coincides to a large extent in more than 150 *Eucalyptus* species. The nature of the rhytidome, however, was taxonomically important and could be used for the identification of species in which external morphological features show great similarity. It has further been found that the grouping of species according to bark characteristics supported a reclassification of species based on morphological characteristics.

The division of the *Eugenia* species of the Old and New World into two separate groups on the basis of wood anatomy (Dadswell & Ingle, 1947), is confirmed by the anatomy of the bark (Chattaway, 1959). This division supports the proposed classification of Merrill and Perry (1938 (a), (b), (c), 1939) which is also supported by other characteristics (Pike, 1956; Schmid, 1972).

The many periderm characteristics that can be used in comparative anatomy [Solereder, 1908; Chattaway 1953, 1955 (a) + (b); Carlquist, 1961; Whitmore, 1962 (a)] are usually very constant and are little influenced by external environmental factors. In this regard Bamber (1962) found that the characteristics of the bark of the Leptospermoideae are of greater taxonomic value than those of the wood of the same group.

Little is known about the seasonal activity and control over the initiation of the phellogen (Zimmerman & Brown, 1974). In this connection the work of Waisel, Lipschitz and Arzee (1967) shows that the phellogen can possess a seasonal rhythm that does not necessarily coincide with that of the vascular cambium.

2. Material and Methods

Both dried and preserved material have been used. Material from different

localities was selected to determine possible environmentally induced variation. Where possible plants of a particular species from at least five different localities were studied quantitatively to determine intraspecific variation. All material was identified by the first author according to the criteria used by Sonder (1862), Engler (1899), Dümmer (1912), Brown (1912), Engler and von Brehmer (1917), Strey (1972) and Van Wyk (1979).

The species discussed in this paper as well as the number of specimens of each species that were examined are given in Table 1. The names of the collectors and the collectors' numbers for the examined specimens can be found in Van Wyk (1978).

Dried material from herbarium sheets was rehydrated by transferring it to distilled water in which it was slowly heated and then boiled for about 30 minutes. Fresh and rehydrated material were fixed in formalin-acetic acid-alcohol (Johansen, 1940).

Fixed material was dehydrated with an ethanol-*n*-propanol-*n*-butanol series and infiltrated and embedded in a monomer mixture of purified glycol methacrylate or unpurified hydroxyethyl methacrylate (HEMA) (Feder & O'Brien, 1968).

Sections 2–4 μm thick were cut with a glass knife on an ultra-microtome and stained with toluidine blue or with periodic acid—Schiff (PAS) stain with

TABLE 1.

Species and number of specimens examined. (Species are grouped according to the results of the study. An asterisk indicates that type material of the species was also studied anatomically)

Species	Number of specimens examined quantitively	Total number of specimens examined
GROUP X		
**Eugenia capensis* (Eckl. + Zeyh.) Sond.	5	30
**E. gueinzii* Sond.	—	1
E. cf. *mossambicensis* Engl.	4	19
**E. natalitia* Sond.	6	40
**E. rudatisii* Engl.	—	1
**E. simii* Dümmer	3	19
GROUP Y		
**E. albanensis* Sond.	—	20
**E. erythrophylla* Strey	5	22
E. pusilla N.E.Br.	—	1
**E. verdoorniae* Van Wyk[1]	5	10
**E. woodii* Dümmer	—	15
**E. zeyheri* Harv.	2	11
**E. zuluensis* Dümmer	3	11

*[1]Previously referred to as *E.* sp. nov. (Van Wyk, 1978).

toluidine blue as a counterstain (Feder & O'Brien, 1968). Schiff's reagent was prepared according to the method in Gurr (1963).

After staining with toluidine blue, sections of material embedded in unpurified HEMA were treated according to the method used by Ruddel (1967).

Freehand sections of fixed material were made to check the constancy of some characteristics for a species. For the localisation of lignified tissue and the periderm the phloroglucinol/hydrochloric acid method was used (Radford, Dickison, Massey & Bell, 1974).

The presence of tannin and suberin was shown with ferrichloride and Sudan IV, respectively (Johansen, 1940).

Only transverse sections through the internodes of the stem were made.

Measurements were taken with an eyepiece micrometer. For practical reasons, a maximum of thirty readings per section were made for a specific characteristic. The mean of these readings is often affected by the few very low or high values that may occur. The median is, however, often a more representative value (Sokal & Rohlf, 1969), and was thus used in this study.

The size and wall thickness of the phellem and phelloid cells were measured as follows:

(a) Phellem cells:
The tangential and radial diameter were respectively measured between the outer edge of the two radial and tangential cell walls of thirty adjacent phellem cells on the same sections. In most cases the first or second row of phellem cells from the phellogen was used. At the same time the maximum thickness of the inner tangential walls was noted.

(b) Phelloid cells:
Measurements were made in the same way as in the case of the phellem cells. Usually the youngest row of phelloids in which the walls of the phelloid cells showed maximum thickness, was used.

Preference was given to those areas on a section where the thickest lignified walls occurred.

3. Results

3.1 *Nature of the periderm*

A periderm is initiated at an early stage in the development of the stem of all the species investigated.

The phellogen and phellem are easy to distinguish, but the phelloderm is poorly developed, usually consisting of a single layer of radially flattened thin-walled cells which are tanniniferous.

The phelloderm shows little variation in all the species and it has not been investigated quantitatively.

The phellem is characteristically that of the Myrtaceae (Metcalfe & Chalk, 1965) and possesses phelloids in which usually only the inner tangential and

radial walls are strongly thickened and lignified. As a result the phelloids appear horseshoe-shaped in cross section. These sclerified walls are usually, but not necessarily always, present in all the phelloids. They are particularly poorly developed in the older phelloid layers of *E. zuluensis* (Fig. 16). Lamellae can usually be distinguished in the thickened walls (Fig. 15). Most often a layer of phellem cells alternates with a layer of phelloids. Multiserial phelloid areas, however, are present in parts of the periderm of some specimens (Fig. 8).

Both the phellem cells and phelloids may be filled with tannin (Fig. 9). Radial phellem rays, one or more cells wide, of thin-walled and sclerified cells, are often present in the phellem (Fig. 14).

Although some lenticels were present on a few slides, especially in those of *E. capensis*, their nature and taxonomic value have not been investigated.

Structurally the periderm of the Southern African *Eugenia* species indicates an affinity with the *Eugenia* species of the New World (*Eugenia* s. str.; Chattaway, 1959).

3.2 *Origin of the periderm*

On the basis of the position in which the first periderm originates in the stem, the *Eugenia* species of Southern Africa can be divided into two groups. These two groups will be referred to as Group X and Group Y (Table 1; Fig. 1).

In Group X the phellogen originates in the parenchyma of the cortex, immediately below the epidermis. No decortification occurs as a result of this periderm (Fig. 6).

In Group Y the phellogen originates in the primary external phloem parenchyma, immediately inside the extraxylary ring of fibres (pericycle) (Figs 11 and 12). The cortex and epidermis shrivel shortly after the formation of the first layer of phellem cells and are pushed off together with the fibre ring (Fig. 13). Especially in freehand sections, older secondary phloem can be confused with the cortex because of the absence of the fibre ring in some specimens. However, secretory cavities are characteristically present in the cortex, but absent from the secondary phloem.

In order to determine the constancy of this characteristic, a number of specimens of most species have been investigated. Where possible, material obtained from the type specimens has been included. From these results it appears that the position in which the periderm initiates in normal stems is constant for a species.

In the same stem, under abnormal conditions, the phellogen can develop in two different positions (Fig. 10). This has been recorded in a specimen of Group X in which part of the superficial layers of the cortex was damaged. In

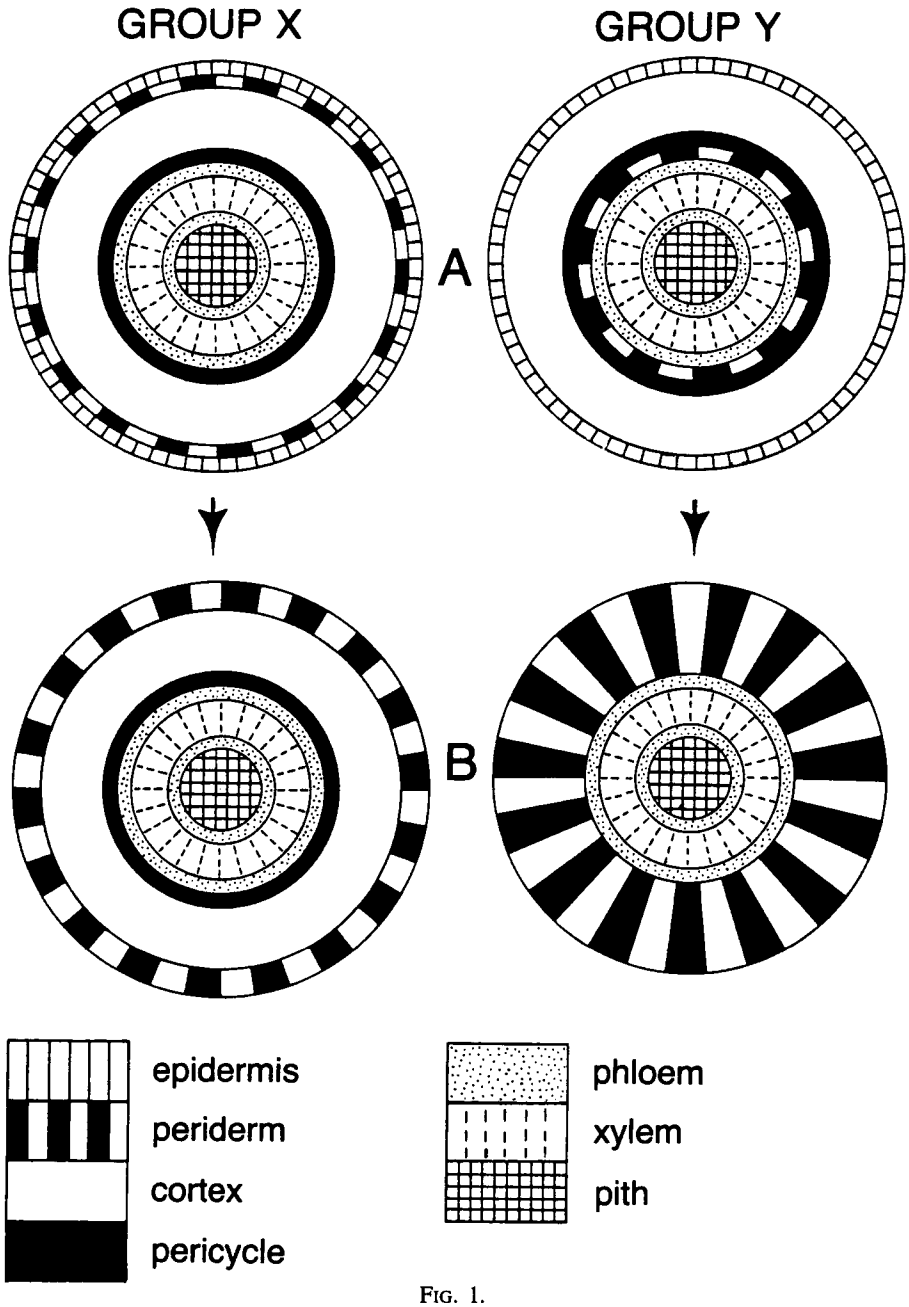

FIG. 1.
Line drawings of stems in transverse section to show the position of the periderm and distribution of the principle tissues in the two species groups which are distinguished. Group X = Periderm superficial in cortex. Group Y = Periderm in primary external phloem. A: Young stem; B: Older stem.

this specimen the periderm is continuous and develops partly subepidermally in the cortex and partly in the primary external phloem—the latter part opposite the damaged cortex.

3.3 *Nature of the cells in the phellem*

3.3.1 Phelloids

In Fig. 2 a scatter diagram is used to correlate the median of the tangential diameter of the phelloids with the median of their radial diameter. From this diagram it seems that the *Eugenia* species can be

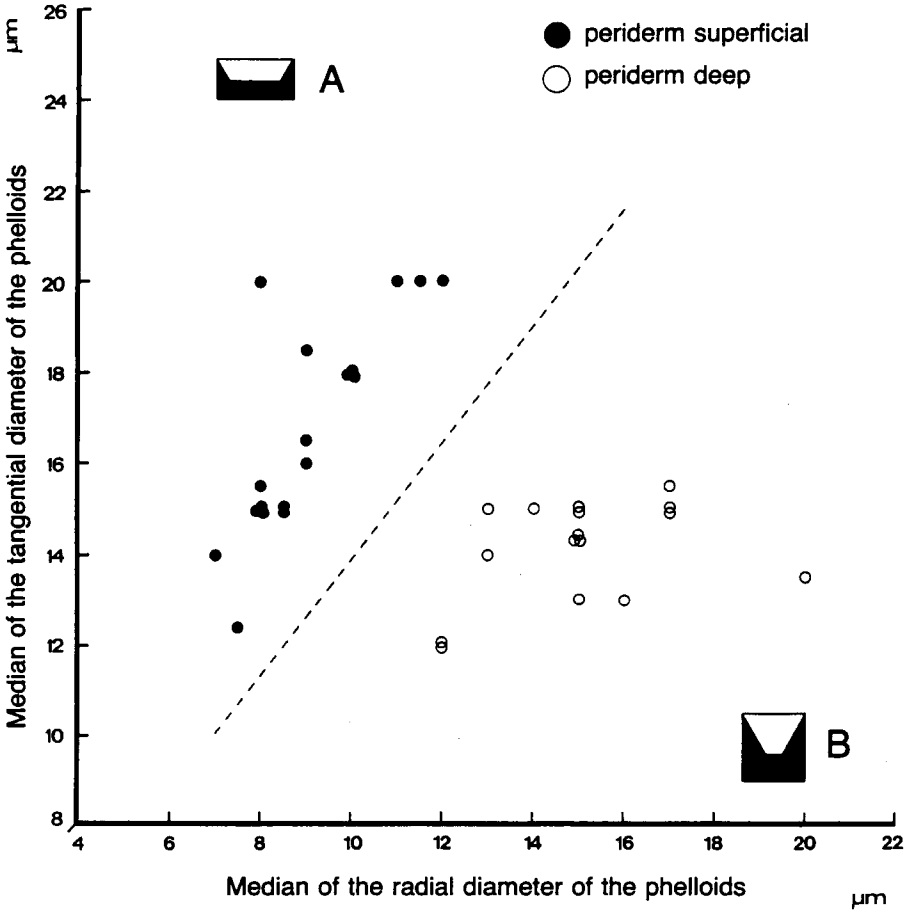

FIG. 2.
Scatter diagram to correlate the radial and tangential diameter of the phelloids. The schematic presentation of the phelloids (A + B) is according to scale and based on the mean of all the median values.

divided into two groups. This division correlates with the position in which the periderm originates. Species belonging to Group X possess phelloids which are radially flattened (Figs 7 and 8) while those of Group Y are radially elongated (Figs 14 and 15). The inner tangential cell walls of Group X are also more thickened than those of Group Y (Figs 7, 8, 14 and 15).

It is further noticeable that the thickened cell walls of Group X are more persistent than those of Group Y. Cell walls of the last mentioned group are often already delignified, or in a state of disintegration in the third phelloid layer from the phellogen (Fig. 15).

Numerous pits are present in the lignified walls of Group X (Fig. 9), while in Group Y they are usually poorly developed (Fig. 15). Lignified cell walls in sections stained with PAS/toluidine blue turned dark red in the case of Group Y but stained lightly in Group X. This may indicate possible differences in the chemical composition of the walls.

The size and wall thickness of the phelloids show little interspecific variation.

The mean of the cell diameter and wall thickness of the median values of the various observations has been separately calculated for all the specimens of Group X and Y and is shown in Table 2.

TABLE 2.
Size of the phelloids. (The mean and standard deviation of the values used in Fig. 2 & Fig. 4)

	Group X	Group Y
Tangential diameter	17,03 ± 2,15 μm	14,16 ± 1,12 μm
Radial diameter	9,15 ± 1,40 μm	15,06 ± 2,09 μm
Thickness of inner tangential walls .	3,76 ± 0,90 μm	5,96 ± 2,23 μm

3.3.2 Phellem cells

According to Fig. 3 it seems that the size of the phellem cells also supports the division of the *Eugenia* species into two groups.

Phellem cells of Group Y are radially flattened, while in Group X they are radially elongated. The median value of the tangential diameter is much the same in both groups. No prominent interspecific differences were noted.

The cell walls of Group X are slightly thicker than those of Group Y.

The values in Table 3 represent the mean cell size and wall thickness calculated from the median values of all the different measurements for all the specimens of Group X and Y.

TABLE 3.
Size of the phellem cells. (The mean and standard deviation of the values used in Fig. 3 & Fig. 4)

	Group X	Group Y
Tangential diameter	16,68 ± 2,84 μm	14,83 ± 1,74 μm
Radial diameter	16,65 ± 3,04 μm	9,20 ± 1,47 μm
Thickness of walls	1,41 ± 0,48 μm	1,0 ± 0 μm

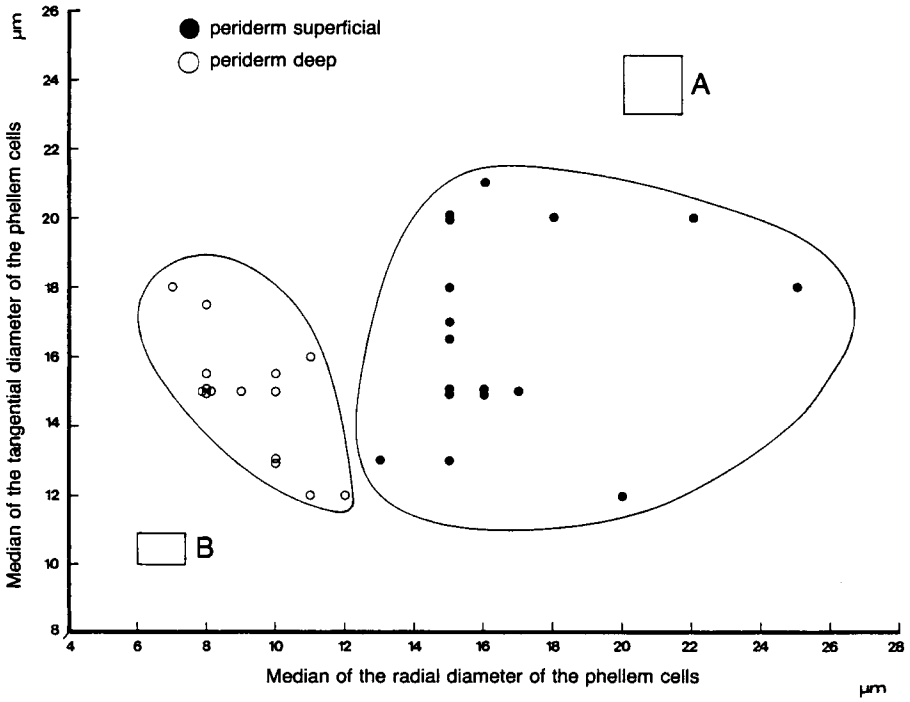

FIG. 3.
Scatter diagram to correlate the radial and tangential diameter of the phellem cells. The schematic presentation of the phellem cells (A + B) is according to scale and based on the mean of all the median values.

3.3 *Structure of the phellem*

The radial diameter of the phellem cells and phelloids is shown by means of a scatter diagram in Fig. 4.

In Group X layers of radially elongated phellem cells alternate with layers of radially flattened phelloid cells. The reverse applies to Group Y. The phellem structure is schematically shown in Fig. 5.

The two different positions in which the periderm originates are thus both correlated with a peculiar structural type of phellem (Figs 7, 8, 14 and 15).

4. Discussion

From a practical viewpoint the position in which the periderm originates is of great taxonomic significance. This characteristic has been investigated in a large number of specimens and was constant for a species. By checking this characteristic in the type specimens the identity of species with hitherto vague taxonomic

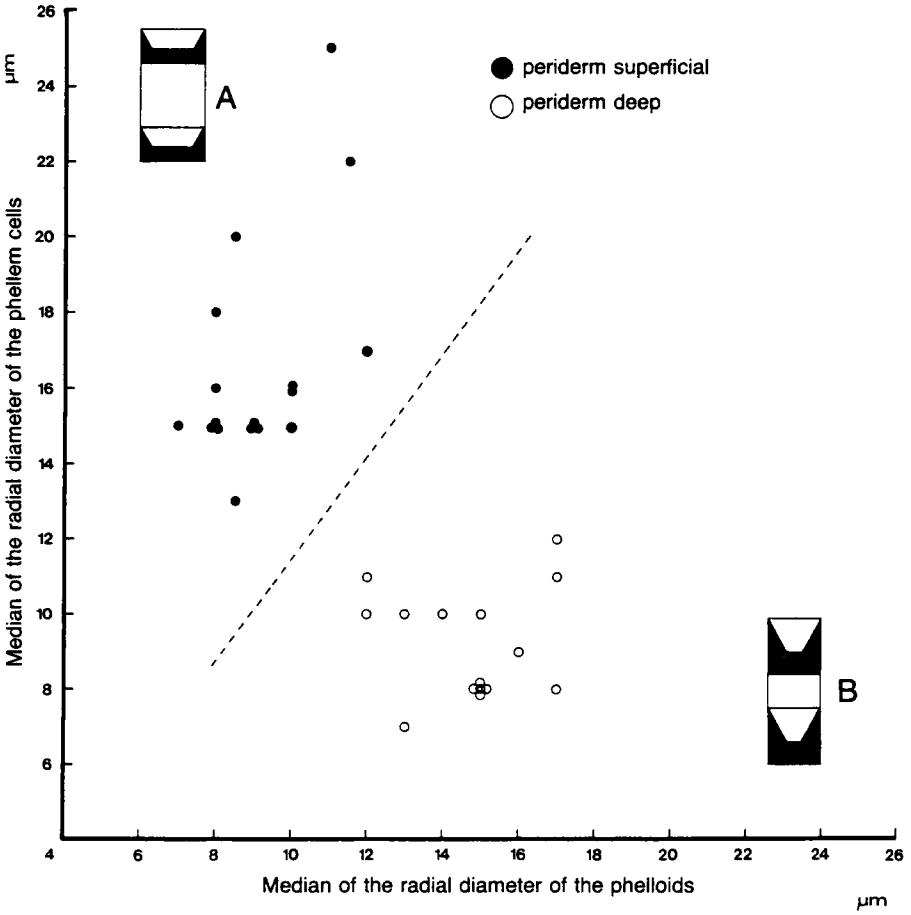

Fig. 4.
Scatter diagram to correlate the radial diameter of the phellem cells with the radial diameter of the phelloids. The schematic presentation of parts of the phellem (A + B) are according to scale and based on the mean of all the median values.

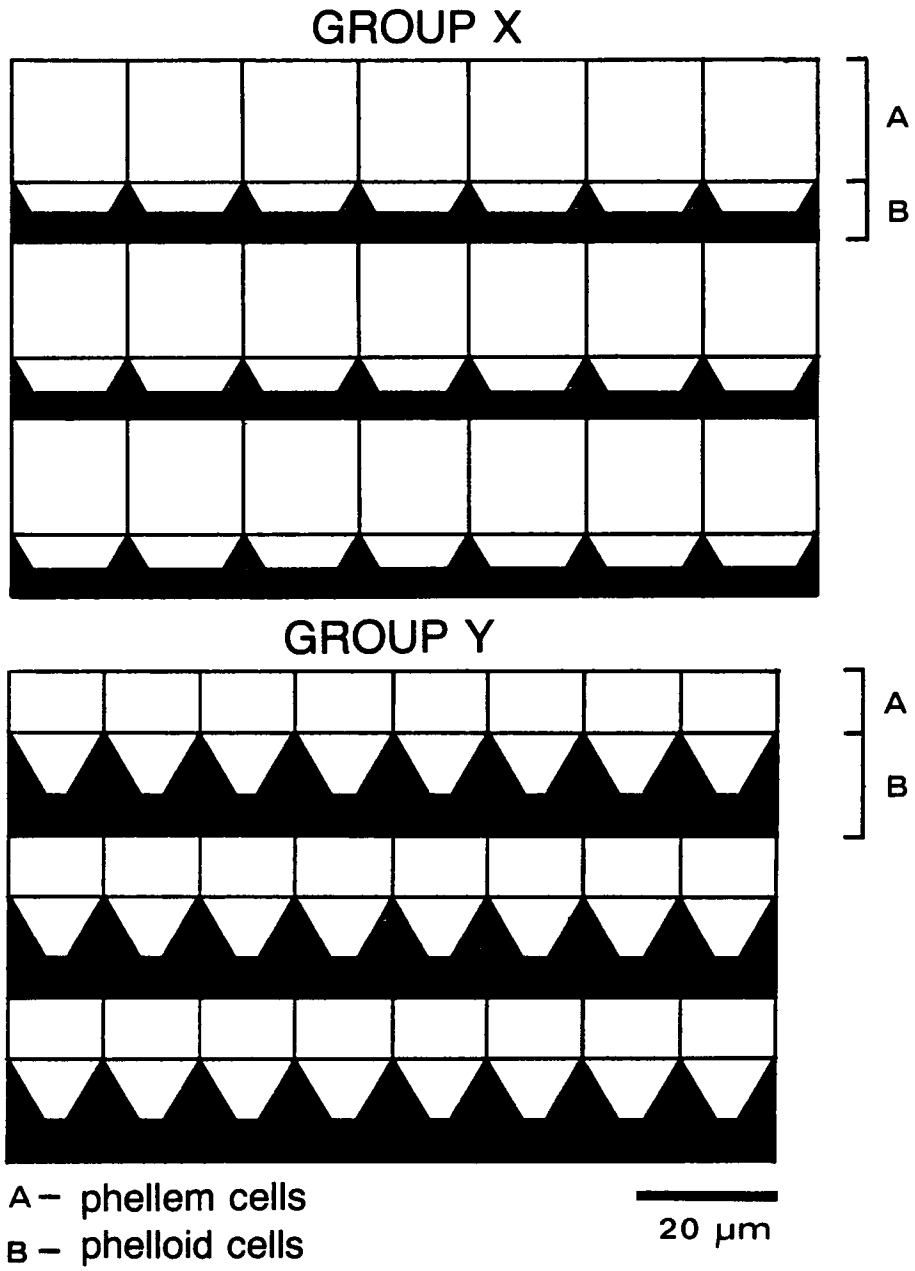

FIG. 5.
Schematic presentation of the structure of the phellem of the first-formed stem periderm in the two species groups; based on the mean values in Tables 2 and 3.

position could be determined. As an example the delimitation of some of the taxa proposed by Dümmer (1912) and White (1977) will next be discussed (Table 4). Taxa which, according to their periderm, belong to Group Y are in CAPITAL letters.

TABLE 4.

A comparison between the treatment of some Southern African *Eugenia* species by different authors. (Taxa belonging to Group Y are in CAPITALS)

Dümmer (1912)	White (1977)
Eugenia capensis (Eckl. + Zeyh.) Sond.	*E. capensis* subsp. *capensis*
E. natalitia Sond.	*E. capensis* subsp. *natalitia* (Sond.) F. White = *E. natalitia*
E. WOODII Dümmer	= *E. WOODII*
E. ZULUENSIS Dümmer	= *E. ZULUENSIS*
E. simii Dümmer	*E. capensis* subsp. *simii* (Dümmer) F. White = *E. simii*
E. ZEYHERI Harv.	*E. capensis* subsp. *ZEYHERI* (Harv.) F. White = *E. ZEYHERI*
E. ALBANENSIS Sond.	*E. capensis* subsp. *ALBANENSIS* (Sond.) F. White = *E. ALBANENSIS*
The brackets indicate that *E. simii* and *E. WOODII* have since the revision been confused with *E. ZEYHERI* and *E. natalitia*, respectively.	This is a list of only some of the proposed new name combinations and their synonyms. Some of the taxa are described in Coates Palgrave (1977) and White (1978).

After the type material of all the species of Dümmer mentioned in Table 4 have been anatomically investigated the following conclusions with regard to the two classifications can be made.

Dümmer proves to be correct in his distinction of *E. natalitia* (Group X) and *E. WOODII* (Group Y) as two separate taxa. Such is also the case with *E. simii* and *E. ZEYHERI* which belong to two different groups.

According to White (1977) *E. ZULUENSIS* and *E. WOODII* are synonyms of *E. capensis* subsp. *natalitia* (=*E. natalitia*).

This is contradicted by the periderm study according to which the first two species belong to Group Y, while *E. natalitia* belongs to Group X.

With regard to the subspecies of *E. capensis* distinguished by White, it is possible that *E. simii* and *E. natalitia* should be allocated subspecific rank. However, according to the periderm results, *E. ALBANENSIS* and *E. ZEYHERI* belong to Group Y and cannot be treated as subspecies of *E. capensis* (Group X).

If these two species are in fact of subspecific rank, it must be from a species in Group Y.

The above examples illustrate the practical value of the observed periderm characteristics. These characteristics are in fact supported by some other anatomical and morphological characteristics.

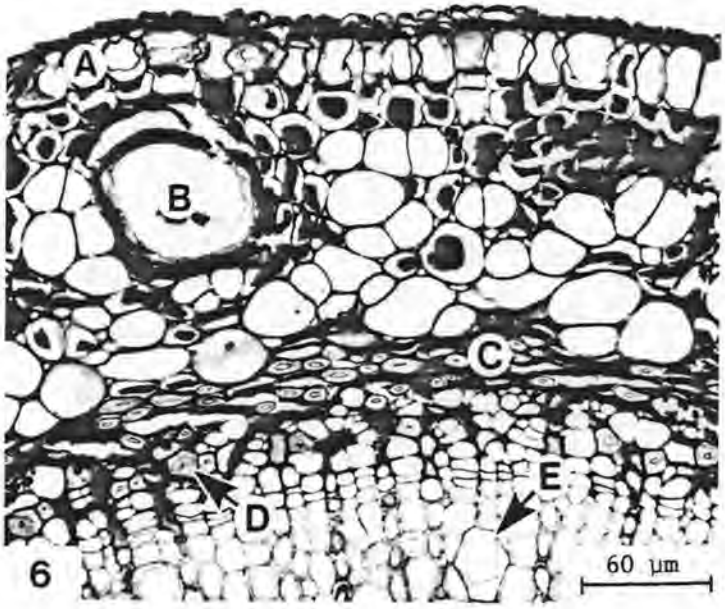

FIG. 6.
Transverse section of the stem of *E. natalitia* to illustrate the periderm (A) which is initiated subepidermally in the cortex; (B) secretory cavity; (C) pericycle with fibres; (D) sclereids in external phloem; (E) crystal bearing idioblast in secondary xylem.

5. CONCLUSIONS

The most important differences between the first-formed stem periderm of Group X and Y are summarised in Table 5. By using the phloroglucinol/hydrochloric acid test on freehand sections of fresh or rehydrated material the nature of the periderm can be ascertained in a quick and easy way. In the herbarium this method is indispensable in order to distinguish between species such as *E. simii* and *E. zeyheri* as well as *E. natalitia* and *E. woodii* which were confused in the past.

It is recommended that the nature of the periderm (especially position in which it is initiated) be investigated for all other members of the genus *Eugenia*. This might prove to be a considerable aid in the identification of specimens which are otherwise often confused.

TABLE 5.

A summary of the expression of some periderm characteristics in the two species groups which are distinguished.

Characteristics	Group X	Group Y
1. Periderm position	superficial in cortex	primary external phloem
2. Phellem cells	radially elongated	radially flattened
3. Phelloids	radially flattened	radially elongated
4. Phelloid walls	3,76 ± 0,9 μm thick	5,96 ± 2,23 μm thick
5. Pits in phelloid walls	numerous	few
6. Nature of thickened walls	relative stable	disintegrate soon after sclerification
7. Thickened walls stained with PAS/toluidine blue	**show little staining**	**stain dark red**

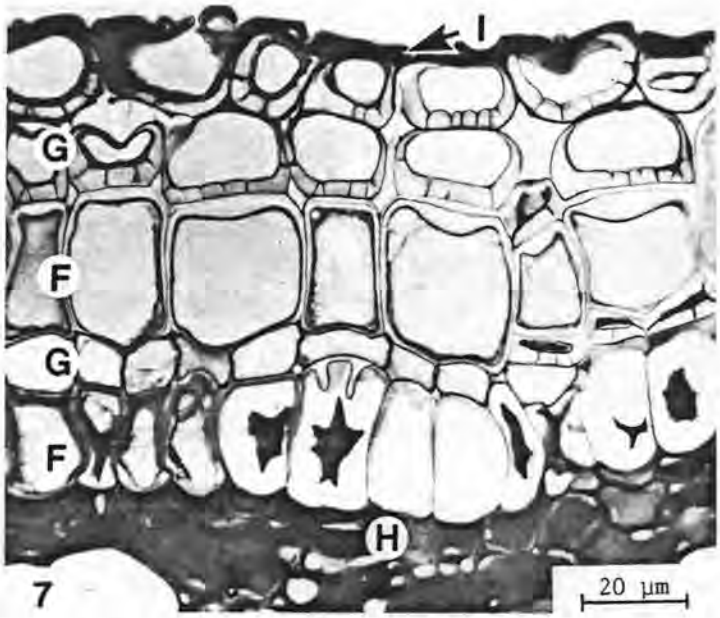

FIG. 7.

Transverse section of the stem of *E.* cf. *mossambicensis* to show the structure of the periderm. (F) radially elongated phellem cells; (G) radially flattened phelloid cells with thickened walls; (H) phellogen; (I) epidermis.

6. ACKNOWLEDGEMENTS

The authors wish to thank the Director and Staff of the Botanical Research Institute in Pretoria for assistance provided in various ways. The financial aid received from the South African C.S.I.R. is acknowledged with thanks.

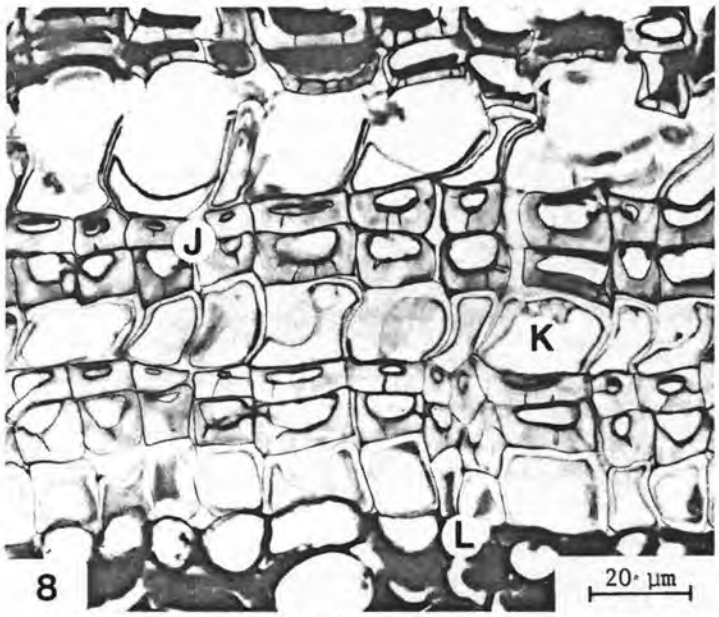

FIG. 8.
Structure of the stem periderm of *E. capensis* as seen in transverse section. Two layers of phelloids (J) alternate with single layers of phellem cells (K). (L) phellogen.

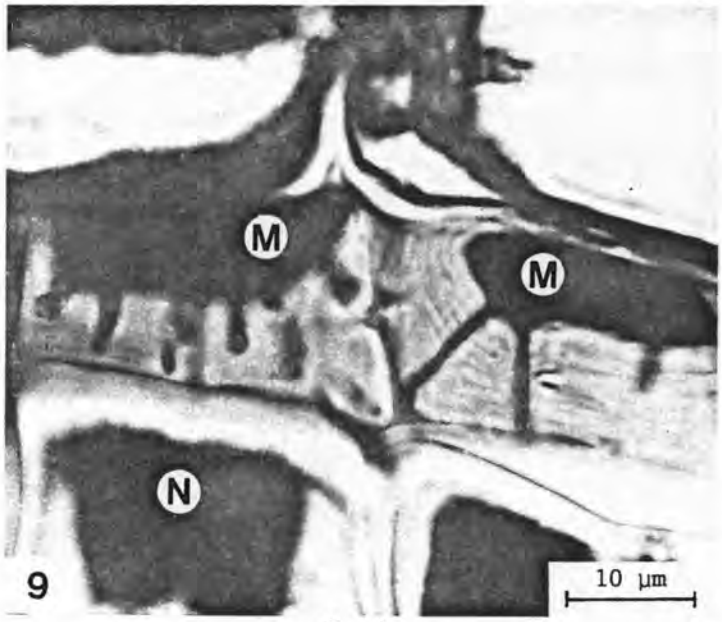

FIG. 9.
Transverse section of the stem periderm of *E. natalitia* to show the numerous pits in the thickened walls of the phelloids (M) which are tanniniferous. (N) phellem cell.

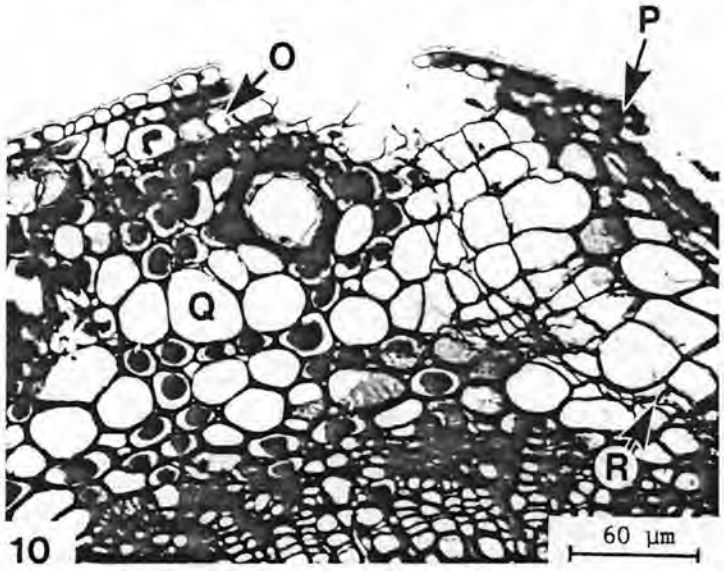

FIG. 10.
Transverse section of the stem of *E. natalitia* to show the superficial phellogen (O) which develops also in the primary external phloem (R) and deeper layers of the cortex (Q) if the superficial cell layers of the stem are damaged (P).

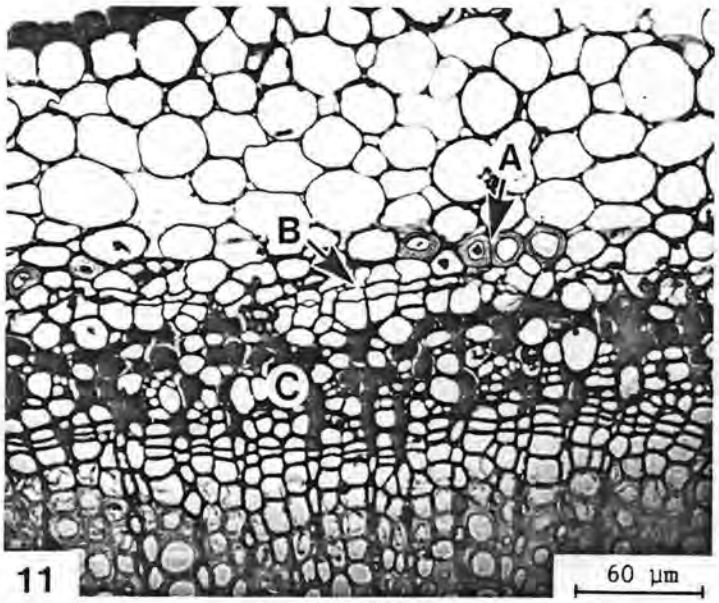

FIG. 11.
Transverse section of the stem of *E. albanensis* to show the initiation of the phellogen (B) in the primary external phloem inside the extraxylary fibre ring (A). (C) secondary external phloem.

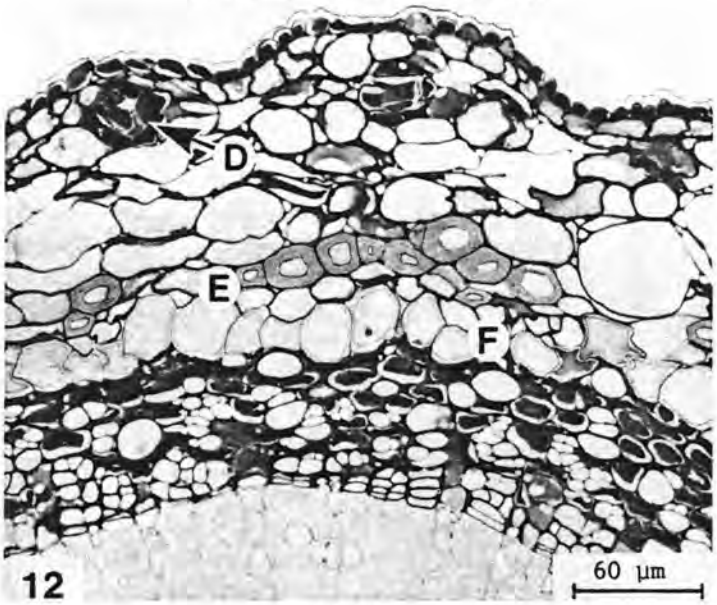

FIG. 12.
Transverse section of an older stem than in Fig. 11 of *E. albanensis* to illustrate the deep seated periderm (F). (E) extraxylary fibre ring; (D) secretory cavity in the cortex.

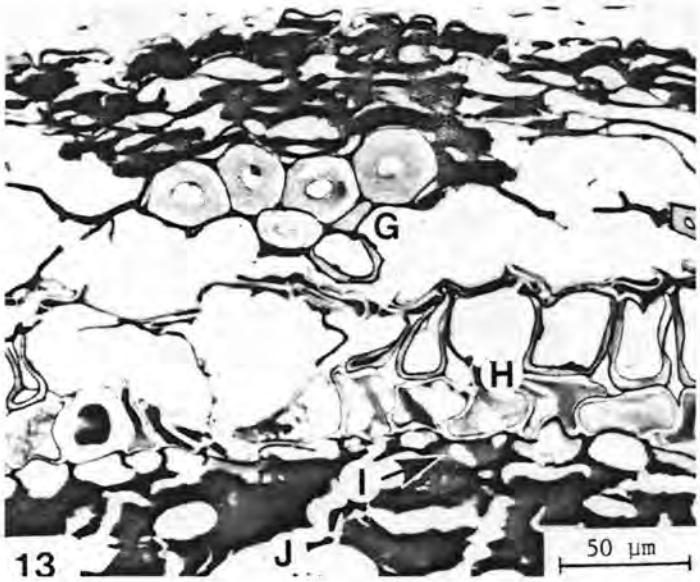

FIG. 13.
Transverse section of the stem of *E. albanensis* to show the decortification as a result of the periderm (H) in the external phloem (J); (G) extraxylary fibres; (I) phellogen.

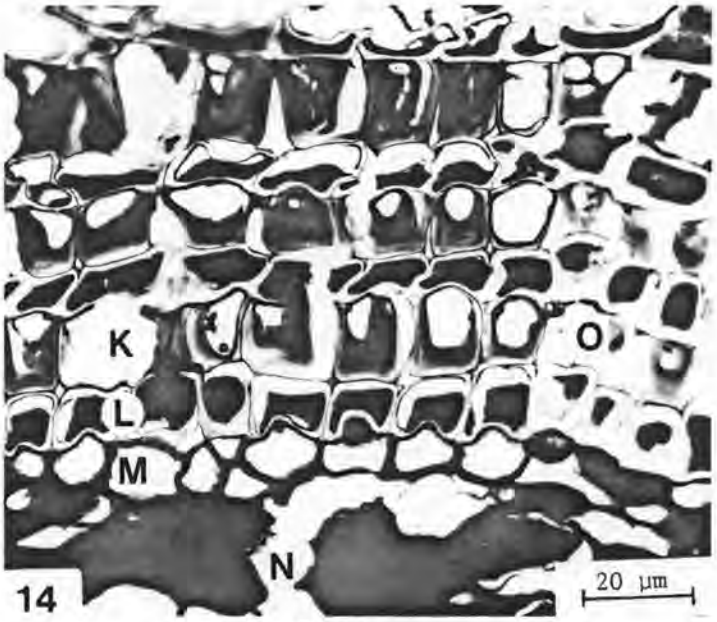

FIG. 14.
Transverse section of the stem periderm of *E. verdoorniae* to illustrate the structure of the periderm. (K) radially elongated phelloids; (L) radially flattened phellem cells; (O) phellem ray; (M) phellogen; (N) secondary external phloem.

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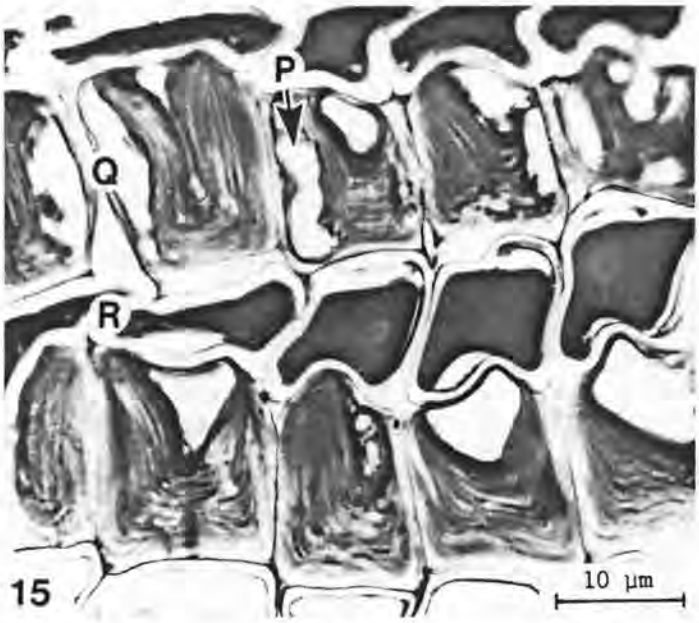

FIG. 15.
Transverse section of the phellem of *E. verdoorniae* to show the layering of the thickened phelloid (Q) walls. These walls disintegrate (P) in older phelloids and show no prominent pits. (R) layer of phellem cells.

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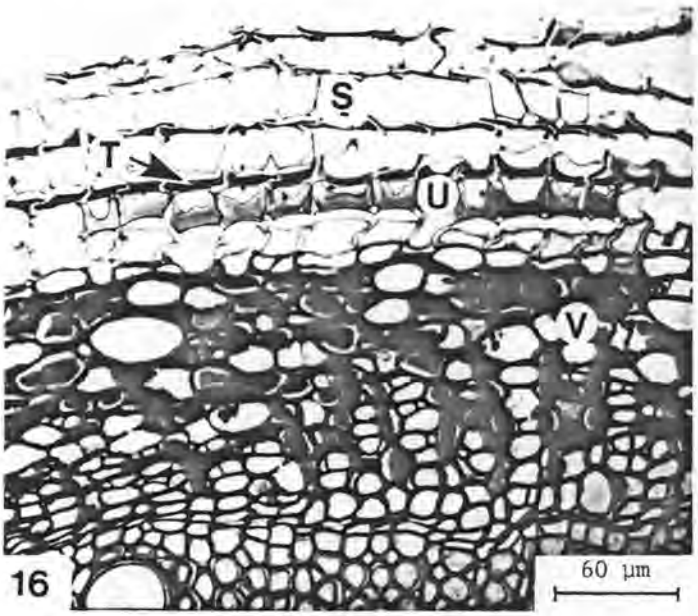

FIG. 16.
Transverse section of the stem of *E. zuluensis*. Note the absence of thickened cell walls in the older phelloid layers (S) and presence in the younger layer (U). (T) phellem cell layer; (V) external phloem.

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CHAPTER 7

STRUCTURE AND TAXONOMIC VALUE OF BARK

The genus *Eugenia* (Myrtaceae) in southern Africa: Structure and taxonomic value of bark

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The anatomy of 60 samples of mature bark representing 12 southern African species of *Eugenia s.str.* was studied. Bark surface patterns are correlated with internal structure and the taxonomic significance of the bark features is explored. Two bark categories are distinguished. Bark type X [*E. capensis* (Eckl. & Zeyh.) Sond., *E. natalitia* Sond., *E. simii* Duemmer and *E. umtamvunensis* Van Wyk] is characterized principally by a smooth or weakly dippled-scaly surface, abundant dilatation tissue (pseudocortex) in the inner bark, phellem with one type of phelloid cell and a well-defined phelloderm. Bark anatomy was found to be useful to separate species. Bark type Y [*E. erythrophylla* Strey, *E. verdoorniae* Van Wyk, *E. woodii* Duemmer, *E. zeyheri* (Harv.) Harv., *E. zuluensis* Duemmer and three undescribed species] is characterized mainly by a flaky surface, little dilatation growth in the inner bark, phellem with two types of phelloids in the phellem and the lack of a distinct phelloderm. With the exception of *E. zuluensis* these species cannot be distinguished on the basis of bark features. Bark characters confirm a previously proposed distinction between two supraspecific groups among native species of *Eugenia*. For diagnostic purposes bark structure is more useful than wood. It is suggested that some of the differences between the two main bark types can be interpreted in terms of the relative rates of formation of xylem and phloem at the vascular cambium.
S. Afr. J. Bot. 1985, 51: 157 – 180

Die anatomie van 60 volwasse basmonsters verteenwoordigend van 12 Suider-Afrikaanse *Eugenia s.str.*-spesies is ondersoek. Basoppervlakpatrone word met anatomiese struktuur in verband gebring en die taksonomiese waarde van die baskenmerke word geëvalueer. Twee baskategorieë word onderskei. Bastipe X [*E. capensis* (Eckl. & Zeyh.) Sond., *E. natalitia* Sond., *E. simii* Duemmer en *E. umtamvunensis* Van Wyk] word gekenmerk deur o.a. 'n basoppervlak wat taamlik glad of swak-pokdalig is, baie uitsettingsweefsel (pseudokorteks) in die binnebas, felleem met 'n enkele tipe felloïedsel en 'n duidelike felloderm. Baskenmerke is nuttig om tussen spesies te onderskei. Bastipe Y [*E. erythrophylla* Strey, *E. verdoorniae* Van Wyk, *E. woodii* Duemmer, *E. zeyheri* (Harv.) Harv., *E. zuluensis* Duemmer en drie onbeskrewe spesies] word gekenmerk deur o.a. 'n basoppervlak wat opvallend afskilfer, min uitsettingsweefsel in die binnebas, felleem met twee tipes felloïedselle en die afwesigheid van 'n duidelike felloderm. Met die uitsondering van *E. zuluensis* kon daar nie op grond van baskenmerke tussen hierdie spesies onderskei word nie. 'n Voorgestelde onderskeid tussen twee supraspesifieke groepe binne die inheemse *Eugenia*-spesies word deur baskenmerke bevestig. Bas blyk ook nuttiger te wees vir diagnostiese doeleindes as hout. Daar word voorgestel dat sommige van die verskille tussen die twee hoofbastipes verklaar kan word aan die hand van die relatiewe tempo waarteen xileem en floëem deur die vaatkambium gevorm word.
S.-Afr. Tydskr. Plantk. 1985, 51: 157 – 180

Keywords: Anatomy, bark, *Eugenia*, Myrtaceae, phloem, taxonomy

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Introduction

In Myrtaceae the mature bole bark exhibits a diversity of surface sculpturings and slash characters. These patterns are usually distinctive for a species and provide an excellent diagnostic feature for field identification. In addition to macroscopic characters, microscopic features of the bark proved to be taxonomically significant. General information on bark structure of Myrtaceae is given in the reference books by Solereder (1908) and Metcalfe & Chalk (1950). The literature is reviewed by Brögli (1926) and Bamber (1962). Roth (1981) provides information on the bark anatomy of many tropical American trees, including a few species of Myrtaceae.

Most bark anatomical studies on Myrtaceae involved members of the subfamily Leptospermoideae, notably the genus *Eucalyptus* L'Hérit. (Brögli 1926; Chattaway 1953, 1955a, b, c, d & e). Bark anatomy of Leptospermoideae is considered to be superior to wood anatomy for the separation of species (Bamber 1962).

The subfamily Myrtoideae includes the two large genera *Eugenia* L. and *Syzygium* Gaertn. Both genera have often been lumped under *Eugenia s.l.* Many species of *Eugenia* mentioned in older literature on bark anatomy (Brögli 1926; Chattaway 1959) are now referred to *Syzygium* or other segregate genera. Macroscopic bark characters are important in the forest identification of species of *Syzygium* and allied genera (Corner 1940; Henderson 1949; Hyland 1983). The anatomy of bark might also assist in the separation of taxa. Unfortunately the microscopic structure of the bark has received little attention (Brögli 1926; Chattaway 1959). Furthermore, little is known about the potential taxonomic value of bark features. In *Eugenia* few species have been studied anatomically (Chattaway 1959; Roth 1981). In a comparative study of *Eugenia s.l.* barks, Chattaway (1959) found significant anatomical differences between two groups of species: *Eugenia* 'A' and *Eugenia* 'B'. Today most species of these groups are assigned to *Eugenia s.str.* and *Syzygium s.l.*, respectively (the problem of generic limits is discussed by Schmid 1972). Possible interspecific differences within the groups were noted by Chattaway (1959), but not discussed.

Characters of the first-formed stem periderm provided the first evidence which led to the recognition of two supraspecific groups, X and Y, within southern African species of *Eugenia* (Van Wyk 1978; Van Wyk *et al.* 1980). These are listed in Table 1. Support for the grouping was subsequently obtained from other anatomical as well as morphological sources (Van Wyk 1978, 1980a; Van Wyk *et al.* 1982), and generic rank has been proposed for both groups (Van Wyk & Botha 1984).

Table 1 Summary of differences between the first-formed stem periderm in species groups X and Y (from Van Wyk 1978; Van Wyk *et al.* 1980)

Character	Group X	Group Y
Periderm position	Subepidermally in cortex	Primary external phloem
Phellem cells	Radially elongated	Radially flattened
Phelloids	Radially flattened	Radially elongated
Pits in phelloid walls	Numerous, conspicuous	Few, obscure
Persistence of thickened phelloid walls	Persistent	Disintegrate soon after sclerification
Staining of thickened phelloid walls with PAS/TB[a]	Show little staining	Dark red

[a]Character states accidentally transposed in Van Wyk *et al.* (1980)

Within species groups X and Y, the delimitation of species received little corroborative support from anatomical evidence (Van Wyk 1978; Van Wyk *et al.* 1982; Van Wyk *et al.* 1983). The discovery that *Eugenia* in southern Africa constitutes a heterogeneous taxon, may nevertheless be considered an important advance towards a natural classification of the species which were often confused in the past. However, the current treatment differs from that of White (1977, 1978) who considered nearly all the species to be closely related.

As a result of the new taxonomic framework established in recent years and outlined above, sufficient order now prevails to commence a comparative study of the mature bark of the species. Possible interspecific differences in bark surface pattern have occasionally been recorded by collectors of *Eugenia* in southern Africa. Whether the bark is flaky or generally smooth has long been used to distinguish between *E. zuluensis* Duemmer and *E. natalitia* Sond. in the forests of Natal. A similar distinction has also been noted between *E. natalitia* and *E. woodii* Duemmer (Van Wyk 1980b). The present work is an attempt to assess bark surface patterns in southern African species of *Eugenia* and to correlate these with internal structure. Special emphasis is laid on the taxonomic significance of the bark characters, particularly at the species level. Interesting tissues or tissue elements are also discussed.

Materials and Methods

Bark features were studied in 12 southern African species of *Eugenia*, including three undescribed taxa provisionally designated *Eugenia* spp. A, B and C. Species names and voucher specimens (only for samples studied anatomically) are listed in Table 2. Localities for most specimens are cited elsewhere (Van Wyk *et al.* 1983). Wood and bark samples were taken from the same plant.

With the exception of *E. simii*, which is a multi-stemmed shrub, all the other species reach tree size. Owing to developmental changes, the bark surface patterns on the main stem(s) of saplings differ from those on mature boles. In this article, however, only the mature bark structure is considered in detail.

Bark samples (with some wood attached) were cut at 0,5 m height from mainly vertical boles not less than 80 mm in diameter, but for *E. simii* from stems 30 – 60 mm in diameter at a position less than 0,5 m high. Above this girth the bark structure does not alter and the bark can be considered as mature. Samples were both fixed in F.A.A. and air-dried.

Table 2 Species of *Eugenia* studied and voucher specimens. Collection numbers are those of the author. Specimens are deposited in the H.G.W.J. Schweickerdt Herbarium (PRU)

Group	Species	Collection numbers
X	*E. capensis* (Eckl. & Zeyh.) Sond.	2586; 2618; 2619; 4507; 4508; 4509; 4510.
X	*E. natalitia* Sond.	950; 2793; 2794; 4252; 4254; 4286.
X	*E. simii* Duemmer	1269; 1270; 4243/1; 4243/2; 4516; 4519; 4520.
X	*E. umtamvunensis* Van Wyk	3631; 4232; 4234.
Y	*E. erythrophylla* Strey	1698; 3342; 4511.
Y	*E. verdoorniae* Van Wyk	1696; 2334; 2335; 4512.
Y	*E. woodii* Duemmer	2517; 2522; 2659; 2805; 2973; 4061; 4255.
Y	*E. zeyheri* (Harv.) Harv.	3126; 3127; 3134; 3135; 3163; 3189.
Y	*E. zuluensis* Duemmer	2662; 2663; 2664; 3263; 3264; 3267; 3268.
Y	*E.* sp. A	2630; 4244/1; 4244/2; 4513; 4514; 4515.
Y	*E.* sp. B	2629; 4239.
Y	*E.* sp. C	5107; 5109.

Anatomical features were studied in transverse, radial and tangential sections as well as in macerations. Unembedded fixed material was softened with steam and cut at 15 – 20 µm on a sliding microtome. Sections were stained with safranin and fast green (Johansen 1940). The presence of lignin and suberin was confirmed with phloroglucinol/hydrochloric acid (Jensen 1962) and Sudan IV (Johansen 1940), respectively. Macerates of the living inner bark were prepared with Schulze's solution (recipe from McLean & Cook 1941) according to the procedure adopted in Van Wyk *et al.* (1983). Sieve plates were examined in hand cut sections of fixed material mounted in resorcin blue (O'Brien & McCully 1981) and viewed with bright field optics. Drawings of sections were made using a camera lucida or projection microscope.

The use of bark sections poses a problem since the rhytidome is brittle and was easily torn apart or lost during sectioning. Interpretation of rhytidome structure was further hampered by the relatively small size of the sections which did not usually show one unit of the repeating pattern of rhytidome construction. To overcome these difficulties a slightly modified version of the simple procedure based on Thorenaar (1926) and employed by Whitmore (1962a) was used. Transverse surfaces of dry bark samples (with attached wood) were cleanly cut with a belt saw and smoothed on an orbital sander equipped with a fine grade abrasive paper. The prepared bark surface was then covered with a thin layer of glycerol, strongly illuminated and examined under the low power of a dissecting microscope. Glycerol was used instead of water (Whitmore 1962a) because the former is not so rapidly absorbed by the dry tissue. Histochemical testing for lignin was done directly on the bark surface. A great deal of structural detail can be obtained by this rapid method.

Photographs were used for comparing bark surface patterns. These were taken from numerous trees growing in a variety of sites over the whole distribution area of a species. A representative selection of the variations seen is illustrated in this article.

Unless otherwise indicated, descriptive terms are those used by Whitmore (1962a, b & c). For some terms synonyms are supplied in brackets. Terminology of the various sclerenchymatous elements in the secondary phloem is according to the proposals of Parameswaran (1980).

Results and Discussion

1. General description of bark structure

By using bark structure the investigated species of *Eugenia* can be clearly separated into two groups corresponding with species groups X and Y. I will therefore refer to bark types X and Y.

Bark surface patterns are illustrated in Figures 1 – 13. Figures 14 – 16 show some of the major differences in bark construction between types X and Y. The main diagnostic features are presented in Table 3. Descriptions for each of the bark types are supplied below. Within-group interspecific bark differences and additional bark features are provided under 2. Bark variation of diagnostic significance at the species level is separately summarized for each bark type in Tables 4 & 5.

(a) Bark type X

Sieve elements. Abundant, randomly scattered as individual cells or small groups between the phloem parenchyma, usually quickly becoming compressed and obliterated. Sieve plates oblique, occasionally transverse; sieve areas (1)2 – 5(8) per plate, more or less equally spaced. Copious slime (P-protein) with numerous small refractive bodies present in the vicinity of the sieve plates. Companion cells narrow and difficult to recognize in longitudinal sections.

Axial phloem parenchyma. Diffuse between sieve tube elements or sometimes in weak tangential lines; consisting of strands of axially elongated thin-walled cells of variable length; not storied.

Phloem rays. Heterogeneous with one or usually more than one row of upright cells; procumbent portion (1)2 – 3(5) cells wide (before dilatation). Uniseriate rays of only upright cells always present. Ray cells thin-walled and abundantly pitted; thick-walled lignified ray parenchyma cells often present adjacent to phloem fibre bundles. Course of rays more or less straight to undulated.

Phloem fibres. Already present close to the cambium, single or in aggregates 2 – 3(5) cells wide radially; randomly distributed or usually in interrupted to fairly continuous concentric layers.

Sclereids. Confined to the dilatation zones and occasionally the non-conducting phloem, scattered as individual cells or irregularly dispersed groups; usually irregularly shaped.

Dilatation tissue. Nearly always well developed, continuous as a pseudocortex beneath the last periderm, inwards interdigitating with the secondary phloem; often greenish coloured in the slash. Composed mainly of parenchyma cells; fibres and obliterated phloem elements occasionally scattered as isolated groups between the matrix of parenchyma cells.

Calcium oxalate crystals. Mainly prismatic; abundant in long axial chambered parenchyma strands; randomly distributed or usually in weak tangential lines throughout the secondary phloem but absent from the rays and pseudocortex. Scattered single parenchyma cells with prismatic or weakly structured druse crystals present in the pseudocortex.

Periderm. Single and superficial or often also with an irregularly spaced deep-seated one cutting off scallop-shaped pieces of tissue; rarely more than two periderms present together. Periderms often slightly undulating, continuous, completely separating living tissues from dead, frequently penetrated by fibres. Phellem stratified, composed of uniseriate concentric layers of thin-walled suberized cells alternating with layers of sclerozed cells (phelloids) of various thicknesses. Phelloid cells of only one type, usually very flattened radially or occasionally more or less square or rectangular; either thickened on the inner tangential cell walls only, or fairly evenly thickened on all walls. Thickened walls with numerous pits, persistent, staining bright red with safranin/fast green. Phellem (at least the most recently formed layers) usually pinkish or reddish-brown on cut transverse surfaces of dried bark samples. Phelloderm

Table 3 Bark types X and Y: Summary of diagnostic features

	Bark type X	Bark type Y
Bark surface	Smooth or weakly dippled-scaly; often conspicuously mottled by whitish microlichen patches	Flaky; microlichens usually absent or inconspicuous
Sloughing	Absent, imperceptible or in localized regions; exposing patches of reddish-brown new bark	Continually over whole surface of bole; exposing cream coloured patches of new bark usually covered by the remains of weathered phloem tissue
Scales/flakes	Scales layer-thick; shed as discrete units composed of intact cut-off phloem tissue covered by periderm	Flakes of periderm; irregularly breaking away mainly owing to weathering processes; cut-off phloem tissue variously decayed and weathered
Rhytidome	Absent or single layer cut-off by scallop-shaped periderms; periderms of adjacent scales do not remain coherent; pseudorhytidome absent	(1)2 – 4(8) sheet-like layers; periderms more or less coherent; pseudorhytidome rarely present
Periderm	Occasionally penetrated by phloem fibres	Apparently not penetrated by phloem fibres
Phellem	Phelloid cells of one type only, with thickened, persistent walls (p-phelloids)	Phelloids of two types; p-phelloids and phelloids with either non-persistent wall thickenings or unthickened walls (n-phelloids)
Phelloderm	Present and well defined	Absent, rarely ill defined
Dilatation tissue	Well developed, forming a pseudocortex	Inconspicuous (dilatation mainly symplastic) or localized in irregular fingers or rarely wedges
Phloem fibres	Single or arranged in aggregates 2 – 3(5) cells wide radially	Single or arranged in aggregates (2)3 – 12(15) cells wide radially
Sieve elements	Sieve areas (1)2 – 5(8) per plate	Sieve areas (1)4 – 10(15) per plate

Table 4 Bark type X: Summary of diagnostic interspecific variations

	E. capensis	*E. natalitia*	*E. simii*	*E. umtamvunensis*
Phellem				
Width	1,0 – 2,5 mm	0,3 – 0,6(0,8) mm		
Colour (transection)	Cream, younger layers often tinged reddish-brown	Pinkish-brown		
Inner bark				
Width	(0,8)1 – 2(2,5) mm			(3)5 – 8(10) mm
Colour (slash)	Creamish-brown or pinkish-brown			Dark reddish-brown
Phloem fibres				
Distribution	Single or in small aggregates randomly distributed or arranged in weakly defined interrupted tangential layers			Single or usually aggregated in fairly continuous concentric layers
Radial diameter	(10)40 – 70(80) µm	(10)20 – 40(45) µm		(10)20 – 50(60) µm

present, usually well developed, parenchymatic.

Rhytidome. Absent or usually with one rhytidome layer present, 1 – 4 mm thick, formed by the cutting off of the pseudocortex and/or non-conducting phloem by scallop-shaped periderms connected to the preceding periderm layer; restricted to localized areas of the bole, occasionally more or less completely covering the bole surface. Pseudorhytidome absent.

Sloughing. As scallop-shaped scales, nearly always one rhytidome layer thick, or tiny inconspicuous scales. Scales with outline more or less circular or irregular; edges of adjacent scales more or less smooth and not continuous at the time of shedding; adhering before sloughing. Loosening of the scales caused by shrinkage owing to dessication of the cut-off mass of tissue, the rotting away of fibres penetrating the inner periderm and the separation of the outer phellem layers of the periderm cutting off the scale. Scales apparently not maintained for a long time; shed as discrete units composed of dead pseudocortex/non-conducting phloem tissue with a layer of periderm on the outside and a very thin layer of periderm on the inner surface; rigid and brittle with the cut-off tissue brownish-black and apparently resistant to decay. Layers of stratified phellem not exfoliating as conspicuous papery sheets.

Surface. Rather smooth or weakly dippled by scattered, more or less scallop-shaped scales. Periderm surface usually finely or coarsely sculptured by longitudinal and occasionally transverse fissures; fissures usually limited to the phellem and often resulting in a grid-cracked pattern. Scroll marks occasionally present. Grey coloured with recently sloughed scales leaving patches of clean reddish-brown new periderm. The bole often conspicuously flecked by white or greyish microlichen patches. Lenticels not observed.

Slash. Pinkish-brown, light brown or rarely dark reddish-brown, usually with a narrow greenish zone just inside the last-formed periderm.

(b) Bark type Y

Sieve elements. With (1)2 – 5(8) sieve areas per plate. Description otherwise similar to bark type X.

Axial phloem parenchyma. As in bark type X.

Phloem rays. More or less straight, rarely slightly undulated, otherwise similar to bark type X.

Phloem fibres. Already present close to the cambium, in aggregates (2)3 – 12(15) cells wide radially; usually distributed in interrupted to fairly concentric layers.

Sclereids. Confined to the non-conducting phloem, scattered as individual cells or irregularly dispersed groups; usually irregularly shaped.

Dilatation tissue. Usually absent, occasionally present as a slight and irregular widening by tangential cell enlargement and limited cell multiplication of some rays and axial phloem parenchyma near the surface, rarely as symmetrical wedges (as seen in transverse section) caused by the regular dilatation of rays and associated axial phloem parenchyma.

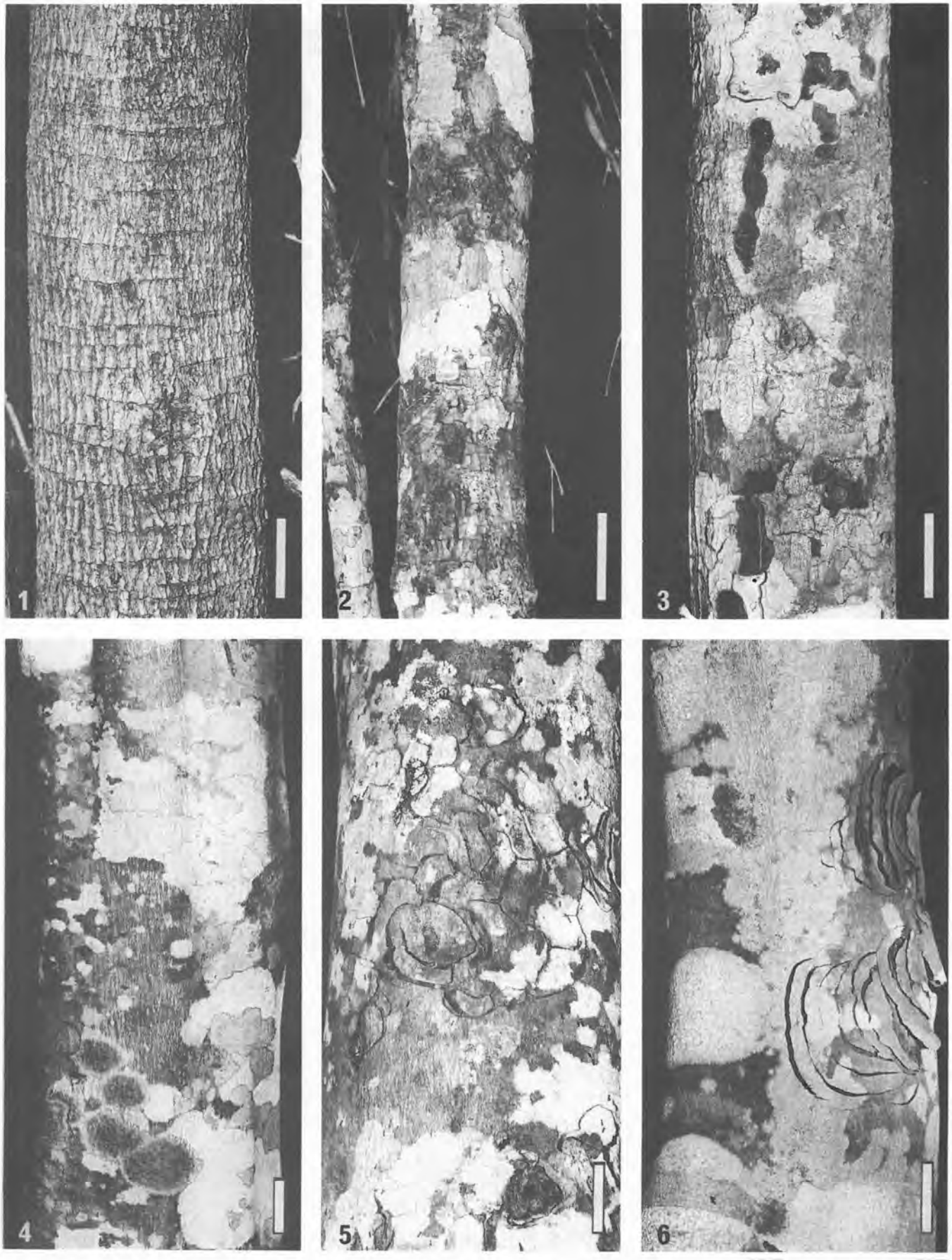
Calcium oxalate crystals. Prismatic; abundant in long axial chambered crystalliferous strands; randomly distributed or usually in weak tangential lines throughout the secondary phloem but absent from the rays. Scattered single parenchyma cells with prismatic crystals often present in the non-conducting phloem.

Periderms. Usually 2 – 8; sequential periderms formed as discontinuous layers connected to the older layers and usually overlapping one another. Periderms rarely slightly undulating, continuous, completely separating living tissues from dead, slightly curved or more or less parallel to the cambium, radially 1 – 2 mm apart; apparently not penetrated by fibres. Phellem stratified, composed of uniseriate concentric layers of thin-walled suberized cells alternating with layers of sclerozed cells (phelloids) of various thicknesses. Phelloid cells of two distinct types based on shape and cell wall characters mainly: either very flattened radially or radially elongated (rectangular to square in transverse section). The former type usually in multiseriate layers, mainly thickened on the inner tangential walls; thickened walls with distinct pits, not conspicuously layered, staining bright red with safranin/fast green, persistent. The latter type usually in uniseriate layers, mainly thickened on the inner

Table 5 Summary of differences between *Eugenia zuluensis* and the remaining species with bark type Y

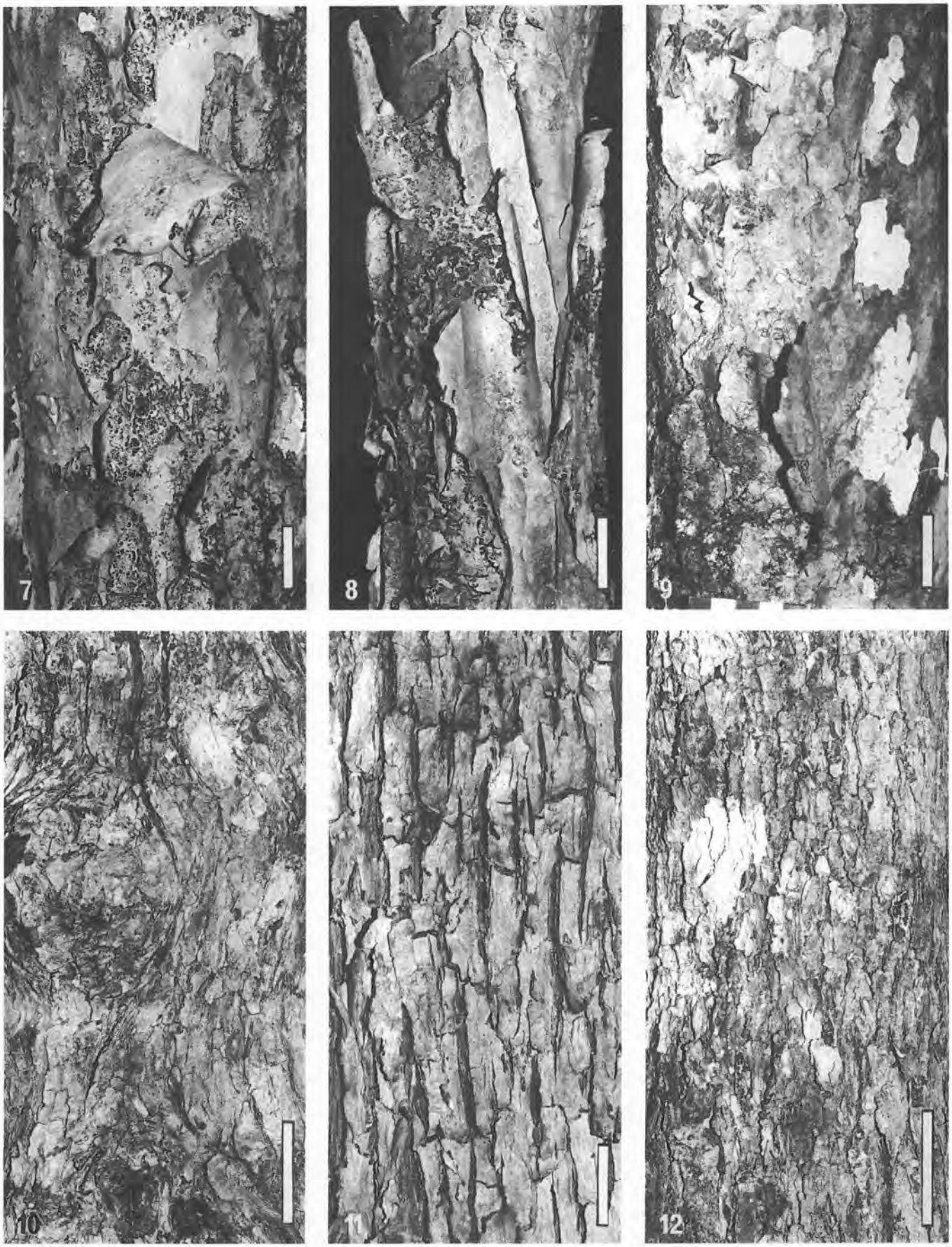
	E. zuluensis	Remaining species
Pseudorhytidome	Conspicuous, peeling off in papery sheets composed of a single phellem cell layer	Absent or inconspicuous; separation of phellem cell layers usually limited to the margins of periderm flakes
Colour of cut-off phloem tissue	Usually yellowish or light brown	Dark blackish-brown
Type of phelloids in phellem	Only n-phelloids observed	Both p- and n-phelloids usually present
Dilatation	Regular funnel-shaped dilatation occasionally present	Regular funnel-shaped dilatation not observed

tangential walls but occasionally evenly on all walls or with thickenings weakly developed or absent; thickened walls with pits obscure, usually distinctly layered, staining reddish-purple or blueish with safranin/fast green, disintegrating soon after sclerification, the walls consequently becoming easily fractured allowing the separation of the suberized layers. Phellem usually cream coloured on cut transverse surfaces of dried bark samples. Phelloderm not conspicuous and apparently absent in some samples.



Figures 1–6 Surface patterns of bark type X. Note conspicuous microlichen patches on most boles. **1.** *Eugenia capensis*. **2.** *E. simii*. **3.** *E. umtamvunensis* — note dark coloured patches exposed by recently shed scales. **4, 5 & 6.** *E. natalitia*; different boles showing no active scaling in 4, typical scaling pattern in 5 and unusual concentric scale formation in 6. Scale line = 300 mm.

Rhytidome. Nearly always present, consisting of (1)2 – 4(8) superimposed sheet-like layers, each 1 – 2 mm thick; formed by a coherent ramifying and anastomosing periderm system, each new periderm taking a shallow course thereby producing a very thin rhytidome layer; usually covering the whole bole surface. Pseudorhytidome often present.



Figures 7 – 12 Surface patterns of bark type Y. Details are extremely variable and only a small selection of the variation is shown. Microlichens are either absent or inconspicuous. **7 & 8.** *Eugenia zuluensis.* **9.** *E.* sp. A; white patches are caused by a fungus. **10.** *E. woodii.* **11.** *E. erythrophylla.* **12.** *E. zeyheri.* Scale line = 300 mm.

Figure 13 Bark surface of *Eugenia* sp. A showing the whitish surface of the outer periderm and the dark coloured remains of cut-off phloem tissue exposed by a recently shed flake of periderm. Phloem tissue is eroded by weathering processes and decay — note its complete absence from the surface of the outer periderm layer. Scale line = 2 mm.

Sloughing. Continually as irregularly outlined flakes of periderm; each flake being the remnants of one rhytidome layer. Flakes adhering before sloughing because of the continuous periderm system. No definite sloughing mechanism present, the pieces of periderm breaking away owing to weathering and fissuring. Cut-off phloem tissue usually becoming blackish-brown and soon almost completely decayed, the resulting spaces adding a spongy consistence to the rhytidome. Sheets of periderm apparently maintained for a long time, often hanging loose before sloughing, occasionally with some weathered remains of the phloem tissue still present on the facing surfaces of successive periderms. Flakes brittle, occasionally with slightly upturned edges. Layers of stratified phellem sometimes conspicuously exfoliating as thin papery sheets or scroll-like pieces (pseudorhytidome).

Surface. Fairly rapidly scaling or breaking off in irregular flakes, locally exposing areas of periderm either smooth-surfaced or often covered by the dark coloured remnants of the cut-off phloem tissue. Fissures usually narrow, longitudinal and transverse, often cutting deep into the rhytidome layers. Scroll marks absent. Bole grey to whitish coloured,sloughed flakes exposing patches of new periderm often coloured blackish or dark brown by the weathered remains of phloem tissue which eventually erodes away exposing the cream coloured periderm below. Microlichens usually absent or inconspicuous. Lenticels not observed.

Slash. Pinkish-brown or light brown, greenish zone inside the last-formed periderm rarely present.

2. Additional notes and discussion on bark anatomical features

(a) Sieve elements, companion cells and axial phloem parenchyma

Although there are several phloem characters which may be applied diagnostically at the species level (Esau 1964, 1979), these are rather neglected in taxonomic studies. Comprehensive comparative studies of the distribution and morphology of sieve elements, companion cells and axial phloem parenchyma concentrate to a large extent on possible trends of phylogenetic specialization (e.g. Zahur 1959; Den Outer 1983)

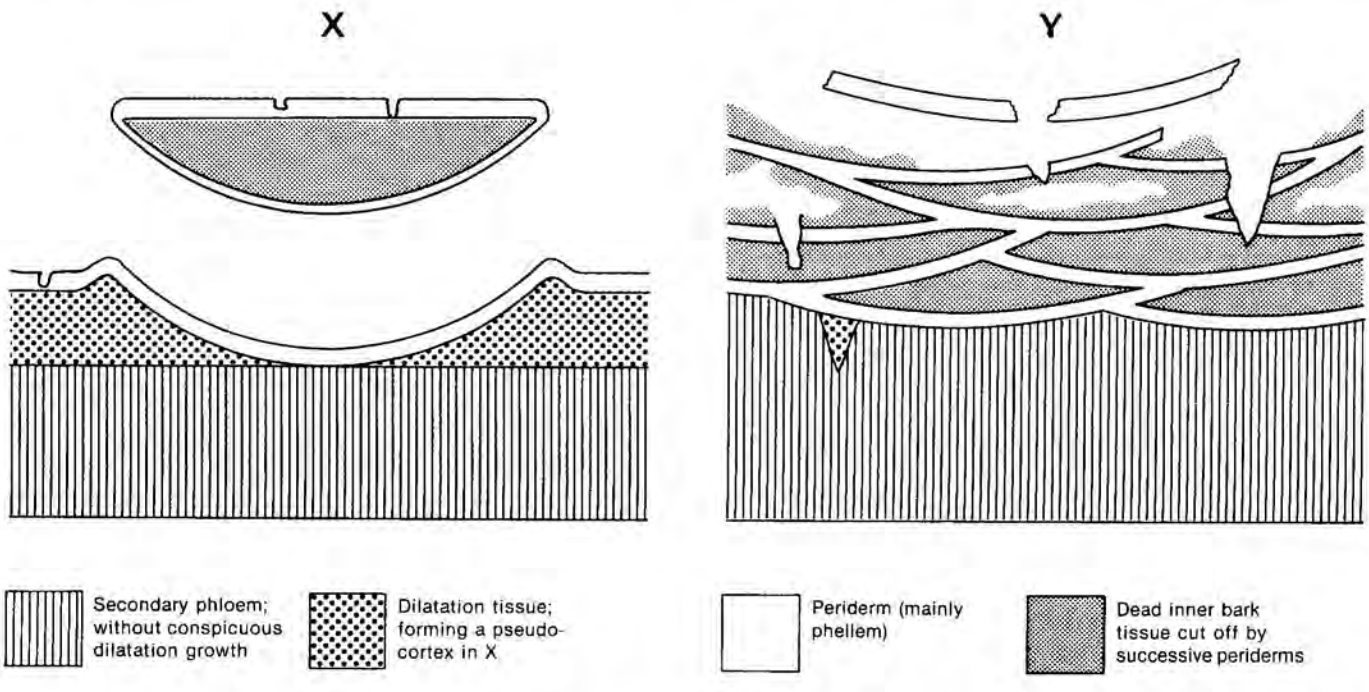


Figure 14 Schematic diagrams of transverse sections of bark illustrating the more conspicuous differences between bark types X and Y. Scale of bark type X just released. Scales of bark type Y are usually shed as flakes of periderm.

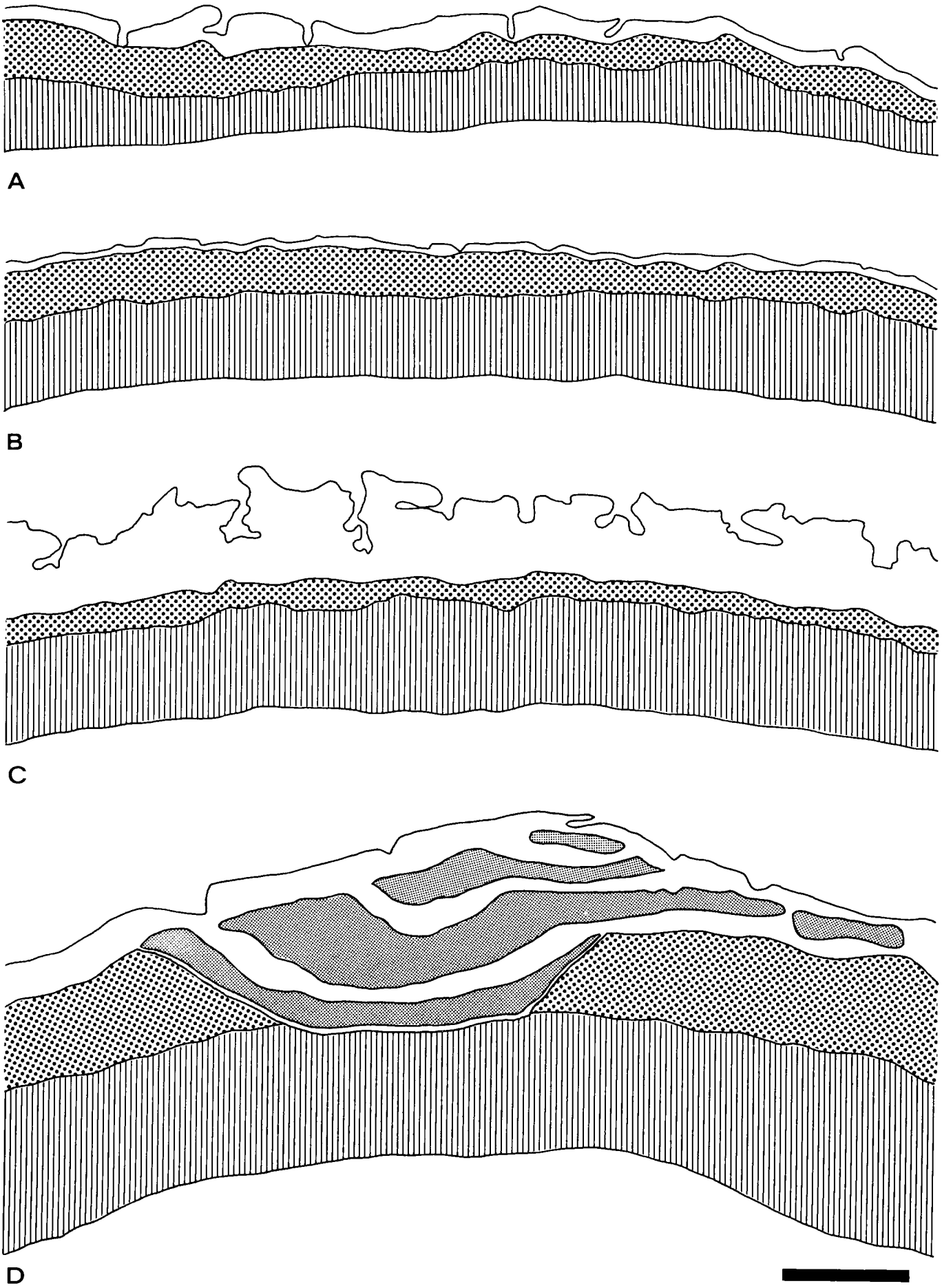


Figure 15A – D Schematic diagrams of the pattern of bark type X as shown in transverse section. See Figure 14 for legend. **A.** *Eugenia simii* (*Van Wyk 4243/1*). **B.** *E. natalitia* (*Van Wyk 2794*). **C.** *E. capensis* (*Van Wyk 2586*) — note relatively thick phellem. **D.** *E. umtamvunensis* (*Van Wyk 4232*) showing a scale traversed by a number of periderms. Scale line = 2 mm.

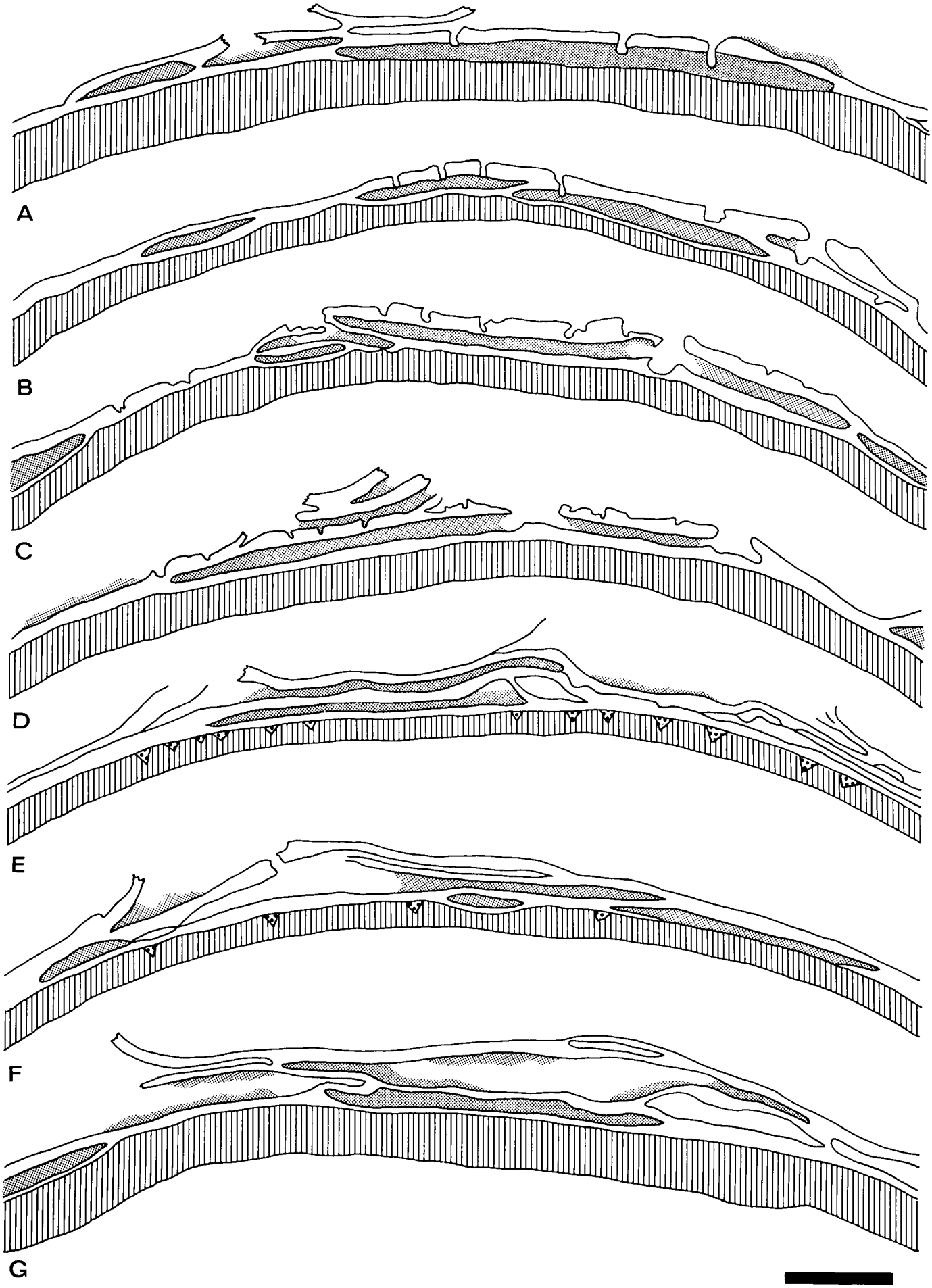


Figure 16A – G Schematic diagrams of the pattern of bark type Y as shown in transverse section. See Figure 14 for legend. **A.** *Eugenia erythrophylla* (*Van Wyk 3342*). **B.** *E.* sp. A (*Van Wyk 4513*). **C.** *E. woodii* (*Van Wyk 2805*). **D.** *E. zeyheri* (*Van Wyk 3134*). **E & F.** *E. zuluensis* (*Van Wyk 2663 & 3267*, respectively). **G.** *E. verdoorniae* (*Van Wyk 4512*). Scale line = 4 mm.

rather than on taxonomic problems.

The relatively thick bark sections used in the present study were not quite suitable for observing axial phloem parenchyma and particularly sieve element and companion cell morphology. It was also not easy to distinguish between parenchyma cells and sieve elements in transections although tanniniferous substances were only present in the former. It is, nevertheless, clear that the overall morphology of these tissue elements conforms to the general secondary phloem description for Myrtoideae by Zahur (1959). Sieve element, companion cell and phloem parenchyma morphology are similar in bark types X and Y. The only conspicuous difference observed is a definite tendency towards the presence of more sieve areas in the compound sieve plates of bark type Y.

Sieve elements and companion cells are clearly discernible only in the conducting part of the phloem ['inner bark' in the sense of Roth (1981) but not of Whitmore (1962a)]. This zone covers only a small cross-sectional area of the bark. The functional period of these cells is short. They lose their callose and become completely obliterated and crushed in the non-conducting phloem. Conducting and non-conducting phloem merge gradually and no distinct layers of collapsed elements are produced to demarcate the two areas.

Growth zones reflecting seasonal variation have been noticed in the secondary phloem of many tree species (Holheide 1951; Lawton & Lawton 1971; Lawton 1972; Roth 1981). The *Eugenia* samples studied did not show any distinct seasonal patterns which may correspond to annual growth zones. Roth (1981) recorded a regular stratification of the secondary phloem in hard and soft bast layers in some Myrtoideae. Concentric rings of soft and hard bast in the native species of *Eugenia* are usually ill defined. Whether one such unit reflects seasonal variation is unknown. According to Roth (1981) the formation of such alternating bands is mainly due to an endogenous rhythm which seems to be independent of climatic periodicity.

Following Zahur (1959) the sieve elements may be classified as types I and II. Sieve areas on the lateral walls of the sieve elements were occasionally present in some samples. Up to 15 lateral sieve areas per element were counted. However, these areas were indistinct and difficult to observe as a result of poor staining with resorcin blue. On the other hand blue staining of sieve areas on sieve plates was intense owing to more conspicuous callose accumulations. Pores in the lateral walls and sieve plates are minute and less than 1 µm in diameter. Sieve element walls are not conspicuously thickened (nacreous) and no tylosoids or distinct secondary partitioning were observed. Nor could any junction complexes be found between sieve tubes as has been reported by Tippett & Hill (1984) in some Leptospermoideae.

In transverse sections companion cells were more conspicuous on account of their small diameter and often more intensely staining cytoplasm (Figure 17). However, they were difficult to locate in longitudinal section and I can therefore not elaborate on their morphology. A definite tendency for these cells to be closely associated with the rays was noted in a few samples.

Tanniniferous compounds frequently accumulate in phloem parenchyma cells. The frequency of these cells varied from sample to sample and tended to be higher in the outer parts of the inner bark. In all the material studied the phloem was considerably more tanniniferous than the adjacent xylem, even in *E. zuluensis* which is considered to be the least tanniniferous of the native species of *Eugenia* (Van Wyk 1978). Judging by the intensity of the stain, the tanniniferous contents of the phloem parenchyma often seem to be less concentrated in *E. zuluensis*. This could explain the particular colour change of the dead phloem tissue in the rhytidome of this species (see 2g).

Starch grains are abundant or almost absent in both tanniniferous and non-tanniniferous cells. Nothing is known, however, about the starch cycle (Lawton & Lawton 1971; Lawton 1972; Roth 1981) in *Eugenia*. The grains are usually simple or up to 8-compound. At least some appear to be hollow (or perhaps thimble-shaped?) thereby resembling the starch grains in the wood (Van Wyk *et al.* 1983) and cotyledons (Van Wyk & Botha 1984). Crystals of calcium oxalate are only deposited in non-tanniniferous phloem parenchyma cells (see 2e).

Parenchyma cell expansion (mainly in the tangential plane) is often pronounced in the non-conducting phloem. The cells in the dilatation zones also become more rounded in longitudinal section. Dilatation is discussed in more detail below (2d). Parenchyma cells are often transformed into sclereids (see 2c) or become meristematic to initiate new periderms (see 2g).

(b) Phloem rays

Ray construction is fairly uniform in Myrtaceae and there are few diagnostic characters. Silica deposition in the ray parenchyma cells is one of the more significant features (Bamber 1962).

In the bark samples studied the morphology of rays in the conducting phloem differs from that in the xylem (Van Wyk *et al.* 1983) in that the rays are composed only of thin-walled non-lignified cells which are more tanniniferous and without disjunctive cell walls. The heterogeneous rays may appear either uniseriate or multiseriate in transverse section — depending on the plane of sectioning. Slightly undulating rays were noticed in most species (particularly samples of *E. simii*) but this does not seem to be of any diagnostic significance. Changes in the course of rays may be caused mainly by the obliteration of sieve tubes and companion cells (Roth 1981).

Abundant deposits of tanniniferous substances are found in the ray cells — even in *E. zuluensis* which has little or no deposits, in at least the procumbent cells of the xylem rays (Van Wyk *et al.* 1983). In *E. zuluensis* the difference in tannin content between the rays on both sides of the thin vascular cambium is striking. Starch grains are usually abundant in ray cells but calcium oxalate crystals and silica aggregates are absent. Sclerosed cells are occasionally found in the dilatation tissue and where fibres are adjacent to ray cells (see 2c).

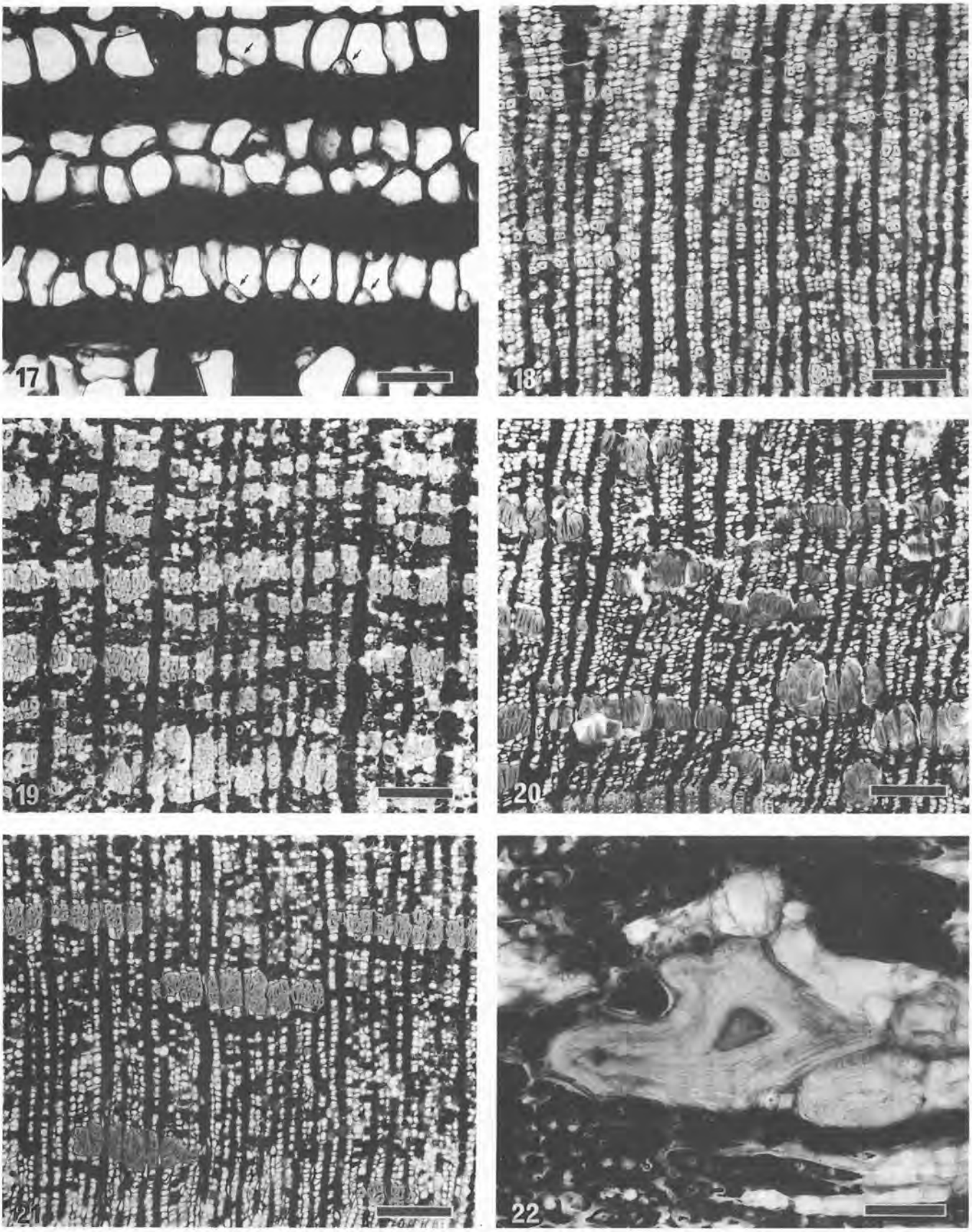
Rays in the non-conducting phloem usually respond to tangential stretching stresses by cell division (mainly the procumbent cells) and tangential cell extension. With the exception of dilatation patterns (see 2d), no constant interspecific differences in ray morphology were noticed.

(c) Sclerenchymatous elements

A redefinition of the sclerenchymatous elements of the secondary phloem based on criteria derived from ontogeny, wall structure, form and growth was recently proposed by Parameswaran (1980). When these definitions were applied, secondary phloem fibres, sclereids and lignified ray parenchyma cells were seen to occur in all the investigated species of *Eugenia*.

Phloem fibres are generally considered to be of taxonomic importance (e.g. Chang 1954; Zahur 1959; Esau 1969 & 1979). Roth (1981) considers the arrangement of these elements seen in transverse section to be the most important bark feature

for diagnostic purposes. However, the present study has shown that the size and distribution of the phloem fibres may vary between different samples of the same species and even from place to place in a single sample. Care should be taken not to draw far ranging taxonomic conclusions when only small numbers of samples are available for study.



Figures 17 – 22 Secondary phloem (inner bark) as seen in transverse section. **17.** *Eugenia zuluensis* (*Van Wyk 2663*) showing sieve tubes with small diameter companion cells (some arrowed) often arranged next to the strongly tanniniferous rays. **18.** *E. natalitia* (*Van Wyk 950*). **19.** *E. umtamvunensis* (*Van Wyk 4232*). **20.** *E. capensis* (*Van Wyk 4507*). **21.** *E. zuluensis* (*Van Wyk 3267*). **22.** *E. erythrophylla* (*Van Wyk 3342*) showing sclereids in the non-conducting phloem. Scale line = 15 µm (Figure 17), 150 µm (Figures 18 – 21) or 40 µm (Figure 22).

In transverse sections of *Eugenia* bark the fibres are recognized as square to polygonal cells with a punctiform lumen (Figures 18 – 21). The cell walls are very thick, lignified, not polylamellate and contain numerous simple pits, usually with slit-shaped apertures. Most fibres are mainly radially flattened causing a conspicuous difference in fibre width between radial and tangential longitudinal sections of the same sample. The fibres are randomly scattered, or more frequently, arranged in tangentially extended groups of variable size and distribution (Figures 18 – 21, 23 & 24). Only rarely are the fibres intermingled with a few crystalliferous strands or lignified ray parenchyma cells.

In radial longitudinal section the fibres appear as a simple system of separate axial strands, but in tangential longitudinal section it is seen that they actually form an intrinsic network ramifying and anastomosing around the rays. The fibres are axially elongated elements obviously derived from the fusiform initials of the vascular cambium and showing apical intrusive growth in the course of development. Their ends are often irregular in outline. Fibre length [(100)200 – 800(900) µm] varies from sample to sample and does not appear to be of any interspecific taxonomic significance. Fibre walls in close contact with crystalliferous strands are often indented by the crystals which become partly embedded in the thickened walls. Septate fibres are absent.

Among the species with bark type X, *Eugenia natalitia* and *E. simii* have a very distinctive bark structure characterized by fibres with a relatively small diameter (Figure 18). These occur singly or in small groups and are dispersed irregularly or in weakly developed and interrupted tangential bands (Figure 23A – D). In *E. umtamvunensis* the fibre diameter tends to be larger and the tangential layers were fairly well defined and almost continuous in two of the samples (Figures 19, 23E & F). Bark from a greater number of trees should be examined to check the frequency of the latter state since this could be useful to distinguish this species from the closely related *E. natalitia*. *E. capensis* clearly differs from the former three species in having fibres with a relatively large radial diameter (Figures 20, 23G & H). These fibres proved to be tougher than those in any of the other investigated species — hence all the sections obtained from this species were ruptured to varying degrees.

Although no sharp distinctions were found between the fibres of bark types X and Y, there is a definite tendency towards the formation of wider and better defined elliptical bundles in the latter group (Figure 24). *E. zuluensis* tends to have fibres arranged in fairly continuous, regular, tangential layers. However, the continuity of the layers varies in samples from different parts of the same tree and even in the same radius from one fibre band to the next (Figures 21, 24E & F). On the other hand, fibres were very sparse in some samples of *E. zeyheri* and *E. erythrophylla*. On the whole, however, the fibres are either not sufficiently different or too variable in size, number and distribution to enable any reliable distinction to be made between species with bark type Y (Figure 24).

Chattaway (1959) gained support for the separation of *Eugenia s.str.* and *Syzygium s.l.* because of the morphology of the secondary phloem fibres. The southern African species of *Eugenia* resemble their New World counterparts in having relatively short (<1000 µm long) phloem fibres with strongly lignified walls (even in the cambial region). Fibre distribution in the New World species also seems to vary from widely spaced groups (often with large radial diameter) to continuous concentric bands (Chattaway 1959; Roth 1981). In some species of *Eugenia* (e.g. *E. uniflora* L. and *E. bahamensis* Kiaersk.) there appear to be no true fibres but columnar groups of sclereids, each formed from a subdivided cambiform strand (Chattaway 1959). Similar sclereids are absent in the native species of *Eugenia*. The occurrence of these and other fibre-replacing sclereids (also called fibre-sclereids or enlarged fibres) in some species of the Leptospermoideae is taxonomically significant (Chattaway 1953, 1955b; Bamber 1962). A comprehensive assessment of the taxonomic value of these cells in Myrtoideae needs to be done.

Sclereids were recorded in all the species of *Eugenia* investigated. They arise in the non-conducting phloem and the dilatation zones (notably the pseudocortex) and develop secondarily from axial phloem parenchyma cells (perhaps also ray parenchyma cells in the pseudocortex). Sclereid formation is preceded by cell enlargement followed by wall thickening and lignification. Apical intrusive growth is absent and the lignified walls are polylamellate and traversed by numerous simple pit canals (Figure 22). A distinct cell lumen (often with tanniniferous contents) is usually retained. The sclereids may vary greatly in size and shape and are irregularly dispersed as individual cells or in small clusters. The walls of the sclereids occasionally undulate. This feature occurs relatively seldom in other groups and appears to be restricted to certain families including Myrtaceae (Roth 1981).

The number of sclereids present varies considerably from sample to sample. Abundant sclereid formation was recorded in some samples of *E. erythrophylla* but was almost absent in others. No interspecific taxonomic significance could be attributed to these cells.

Lignified ray parenchyma cells (ray-sclereids) were noticed sporadically in all the investigated species. These cells are formed from ray parenchyma and only develop where rays abut on fibres or traverse fibre bundles. There is no enlargement of the ray cells, only the cell walls become thick and lignified (not polylamellate). These lignified parenchyma cells are usually tanniniferous and identical to the ray cells in the wood.

(d) Dilatation tissue

Growth of xylem and phloem at the vascular cambium sets up a tangential strain in all the tissues outside the cambial cylinder. One way in which the bark accommodates this is by the formation of dilatation (expansion) tissue. Dilatation growth patterns are often diagnostic for a species and may be used for identification. In this regard bark types X and Y are markedly different (Figure 14).

In bark type X a large proportion of the tangential growth is by the formation of dilatation tissue. This tissue occurs in a conspicuous more or less continuous cortex-like band at the surface of the non-conducting phloem (Figures 14, 15 & 25). Whitmore (1962a & b, 1963) considered a similar tissue in the bark of some Dipterocarpaceae and Fagaceae to be of secondary origin and called it the pseudocortex. According to Whitmore (1963) several previous authors have erred by explicitly or implicitly assuming it to be the primary cortex of the stem. Whitmore's interpretation of the pseudocortex was questioned by Esau (1969) who also suspected it to be the true cortex.

To clarify some of the uncertainties surrounding the concept of the pseudocortex, an attempt was made during the present study to trace the origin of this tissue in some of the species. For this purpose hand-cut sections were prepared from young and progressively older stems of *E. capensis*, *E. natalitia* and *E. simii*. Bark development was followed from the initiation of the first periderm in the young stem to the stage when the

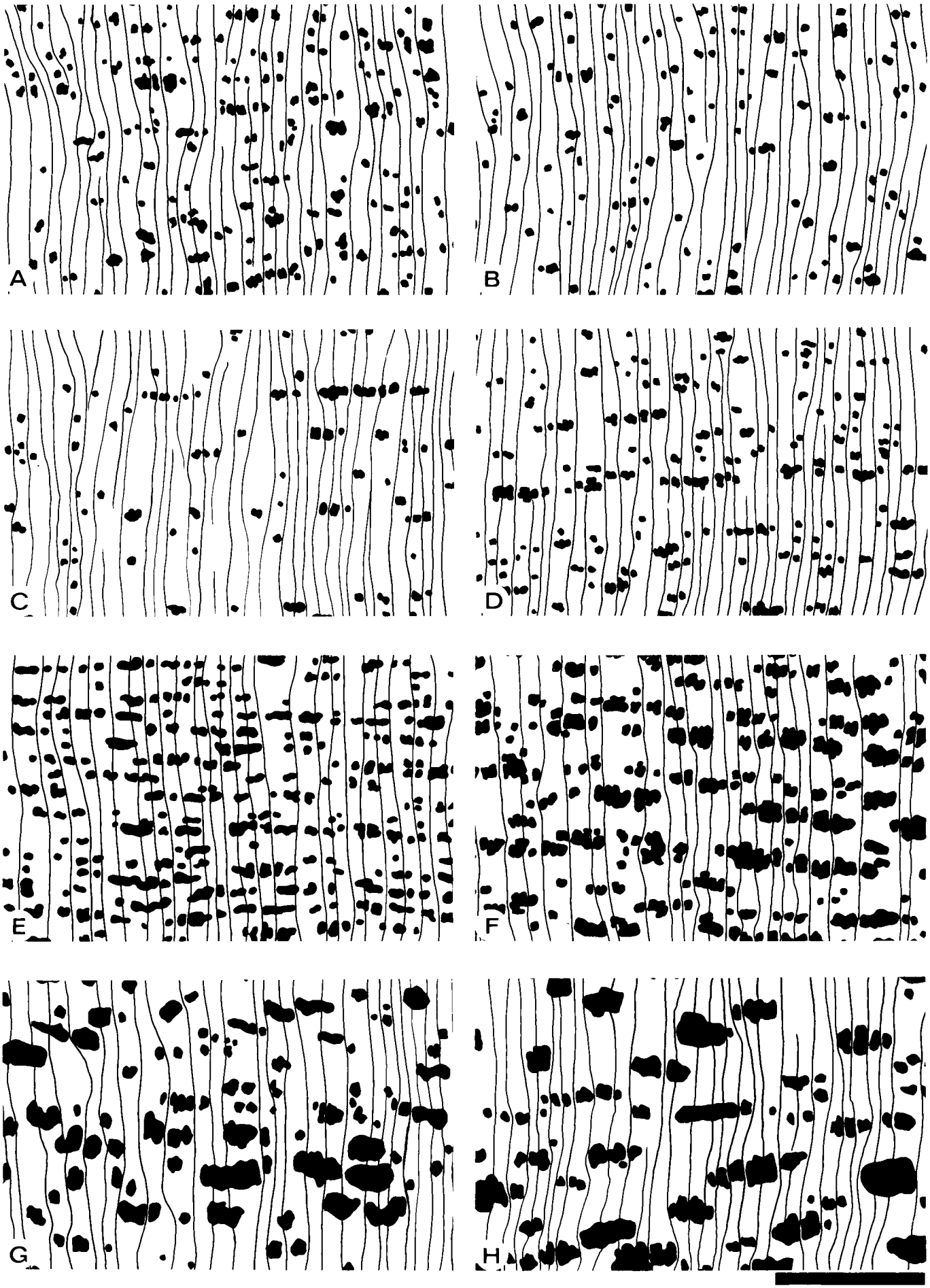


Figure 23A – H Arrangement of fibres and fibre bundles in species with bark type X as seen in transverse section of the inner bark (before conspicuous dilatation growth). **A & B.** *Eugenia simii* (*Van Wyk 4519 & 4516*, respectively). **C & D.** *E. natalitia* (*Van Wyk 2793 & 950*, respectively). **E & F.** *E. umtamvunensis* (*Van Wyk 4232 & 3631*, respectively). **G & H.** *E. capensis* (*Van Wyk 4508 & 4507*, respectively). Scale line = 500 µm.

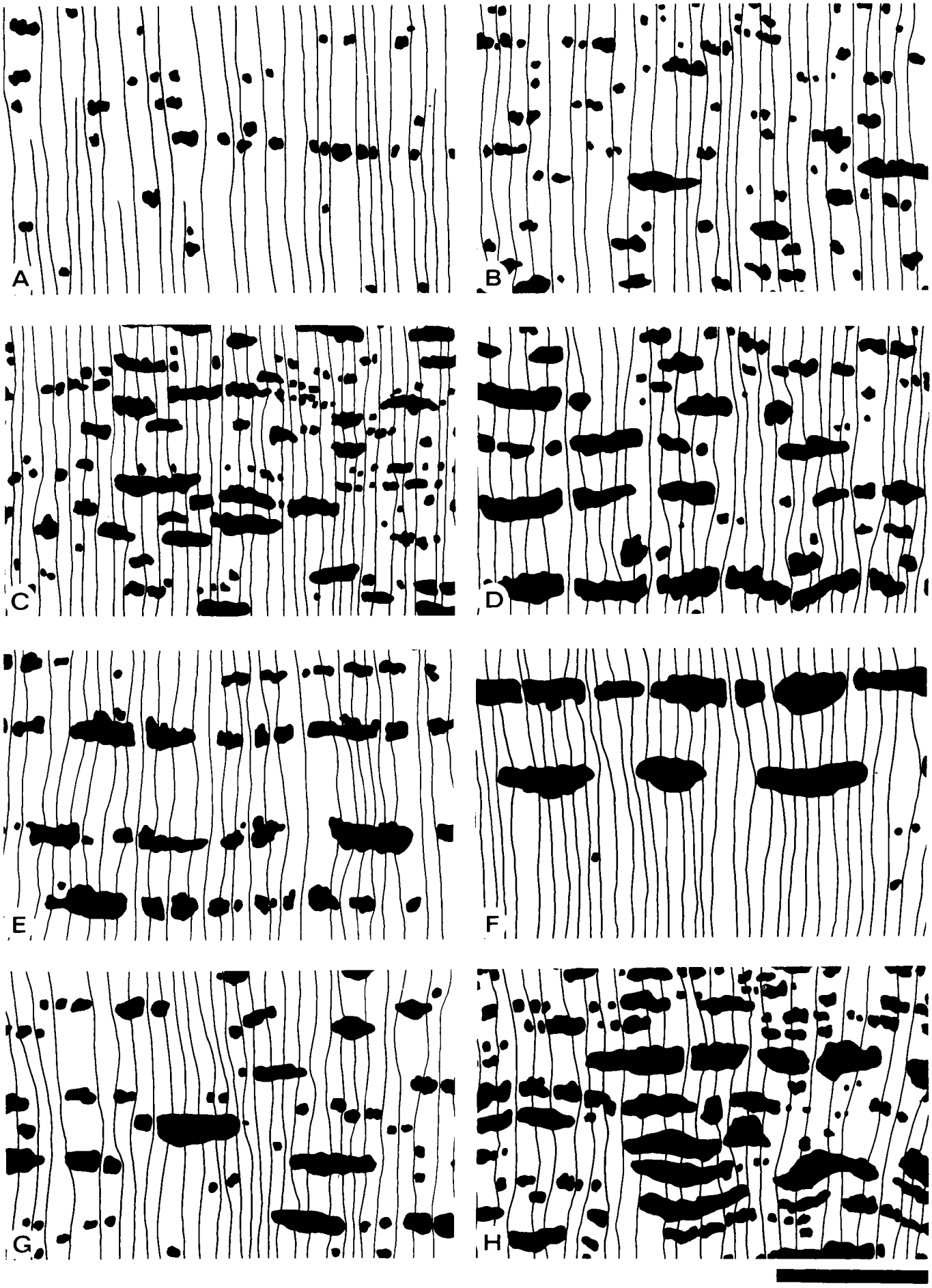


Figure 24A – H Arrangement of fibres and fibre bundles in species with bark type Y as seen in transverse section of the inner bark (before dilatation growth). **A.** *Eugenia erythrophylla* (*Van Wyk 1698*). **B.** *E. woodii* (*Van Wyk 2659*). **C.** *E.* sp. A (*Van Wyk 4515*). **D.** *E.* sp. B (*Van Wyk 2629*). **E & F.** *E. zuluensis* (*Van Wyk 2664 & 3267*, respectively). **G.** *E. zeyheri* (*Van Wyk 3127*). **H.** *E. verdoorniae* (*Van Wyk 4512*). Scale line = 500 µm.

mature bark pattern is established on old stems.

The first-formed periderm is initiated at an early stage in the cortex, immediately below the epidermis (Van Wyk *et al.* 1980). No decortification occurs. Secretory cavities are characteristically present in the cortex and therefore serve as useful markers to trace the presence of this tissue. Yellowish-green pigment (chlorophyll?) occurs in the starch-containing plastids in the parenchyma cells of the cortex and phloem rays. An interrupted or continuous cylinder of extraxylary (apparently protophloem) fibres delimits the phloem from the cortex in *E. natalitia* and *E. simii* but is lacking in *E. capensis*. Druse crystals are occasionally present in the cortex.

The first-formed periderm (at least in part) and primary cortex are maintained for perhaps a number of years. During this period the cortex adjusts to the secondary increase in circumference by symplastic tangential expansion and cell multiplication. The extraxylary fibre cylinder is disrupted during the expansion of the cortex making it difficult to locate the now scattered fibres in older stems. Secretory cavities similarly become widely separated and could easily be missed unless a number of different sections are examined. Despite these difficulties, fibres as well as the tanniniferous remains of secretory cavities were still found in stems up to about 60 mm in diameter. Outer regions of the secondary phloem also start to dilate. The ray tissue merges into the cortical tissue so gradually that it is difficult to determine where rays end and cortex begins. Up to this stage there can be no doubt that the parenchyma tissue between the phloem and the periderm has been derived mainly from the primary cortex. With further increase in age, however, this state changes owing to the increasing activity of successive periderms.

Small scale-like successive periderms which penetrate deeper into the cortex but remain in contact with the older periderm develop occasionally during the first years. These periderms cut off thin layers of cortex tissue (the scales are often imperceptible) and are sporadically scattered over the surface of the stem. Initially the cut-off tissue is quickly replaced by cell proliferation of the remaining cortex cells. The secretory cavities gradually diminish in number and are eventually lost because of their peripheral displacement, being cut off by the successive periderms. There is no secondary replacement of secretory cavities.

The occasional scales (usually not conspicuous in *E. capensis*) gradually increase in size and frequency. By the time the mature bark pattern becomes established, newly formed scallop-shaped periderms cut deeply into the cortex and often also into the non-conducting secondary phloem. Cortex and phloem tissues removed by the scales are now mainly replaced by proliferation of phloem ray cells, from the tangentially dilated outer ends of the rays. Considerable proliferation of the ray parenchyma leads to the disruption of the regular radial arrangement of the secondary phloem. This results in a parenchyma-dominated zone of tissue interdigiting with the non-conducting phloem. An often well developed parenchymatous phelloderm usually merges imperceptibly with the outermost region of this zone. I consider this zone of dilatation tissue to be the so-called pseudocortex. It contains scattered remains of the disrupted secondary phloem and is mainly of secondary origin. This agrees with the interpretation of Whitmore (1962a, 1963).

However, the issue is not that simple. Usually, not all parts of the mature bole bark are affected simultaneously by the scales. Smooth surfaced areas often separate regions of active scaling (e.g. Figures 5 & 6). Some of the former regions obviously retain elements derived from the original cortex much longer than the latter regions. It is, therefore, possible that the dilatation zone in a bark may be made up of a mosaic of both mainly primarily and mainly secondarily derived tissue. 'Mixing' of cells from these latter tissues evidently occurs and it is doubtful whether all the elements derived from the original cortex are eventually lost. Even on a bole that is actively forming scales over most of its surface (often in *E. umtamvunensis*), primary cortex tissue may be retained in the wedge-shaped ridges (often forming scroll marks) of tissue which remain between adjacent scallop-shaped scales.

It should be apparent that the cortex-like zone of dilatation tissue is from a different origin in young and mature samples of bark type X. The transition is gradual and intermediate states occur. Authors claiming that this zone of dilatation tissue is derived mainly from the original cortex, could therefore be correct if their observations refer to younger stems only. To avoid confusion the term pseudocortex in bark descriptions should be used only for dilatation tissue derived mainly from the secondary phloem ('pseudocortex' is also used in quite a different context in certain algae — see e.g. Jackson 1928).

The formation and sloughing of scales in bark type X are usually a cyclical process and the development of the pseudocortex varies during the cycle. It is nearly always well developed in those parts of the bole with a smooth surface but almost absent from parts where sloughing occurs. Once the pseudocortex has sloughed, it may take a long time to grow another.

In *Eugenia* the pseudocortex is 0,25 – 1,0 mm thick and occupies roughly 25 – 40(60)% of the living inner bark diameter (Figure 15) (see 2h for slash features). The parenchyma cells are very uniform in size, isodiametric in radial section and slightly elongated tangentially in transverse section. Intercellular spaces are occasionally present, mainly towards the phelloderm. A large proportion of the cells is tanniniferous and druse crystals as well as sclereids (see 2e & 2c respectively) are usually present (Figure 25). Secretory cavities are typically absent. Tanniniferous remains of secretory cavities were rarely present in some samples of *E. simii*, but these belong to the tissue of the original cortex which seems to be more persistent in the relatively thin stems of this shrubby species.

The transition between the non-conducting phloem and pseudocortex is often remarkably sharp, especially when viewed in radial section (Figure 25). The distinction is mainly due to the apparent absence of axially elongated elements in the pseudocortex — notably the lack of crystalliferous parenchyma strands which are abundant in the rest of the secondary phloem. However, close inspection of the pseudocortex reveals small inclusions of obliterated crystalliferous strands and other phloem tissue (which can no longer be easily distinguished) set in the mass of parenchyma cells. Phloem fibres are very sparse in the pseudocortex and this seems somewhat unexpected. It could perhaps be explained by assuming that the fibres are widely separated by the massive multiplication of the parenchyma cells and are therefore not readily detectable in thin sections. Careful dissection of the bark in some Dipterocarpaceae suggests that the phloem fibres in the pseudocortex break up into short peripheral fragments (Whitmore 1962a). No conclusive evidence for this was found in *Eugenia*.

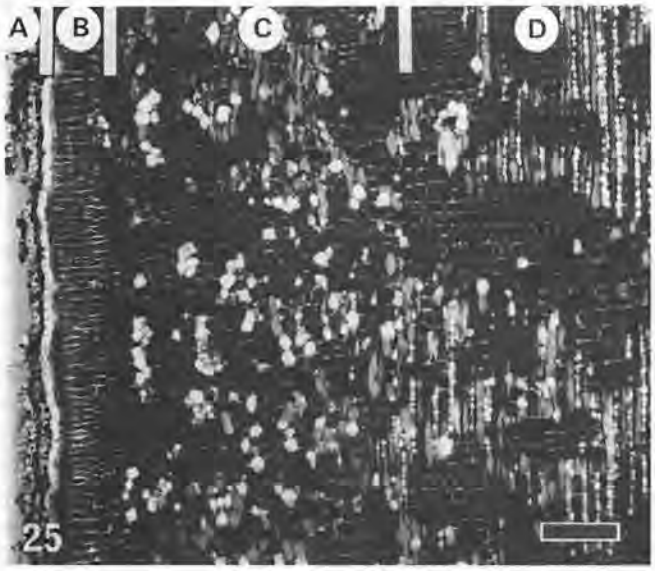
Bark type Y shows little or no dilatation (Figures 14 & 16). The first-formed periderm originates in the primary external phloem resulting in complete decortification (Van Wyk 1978; Van Wyk *et al.* 1980). Dilatation is often more obvious in younger stems but becomes obscure later when successive

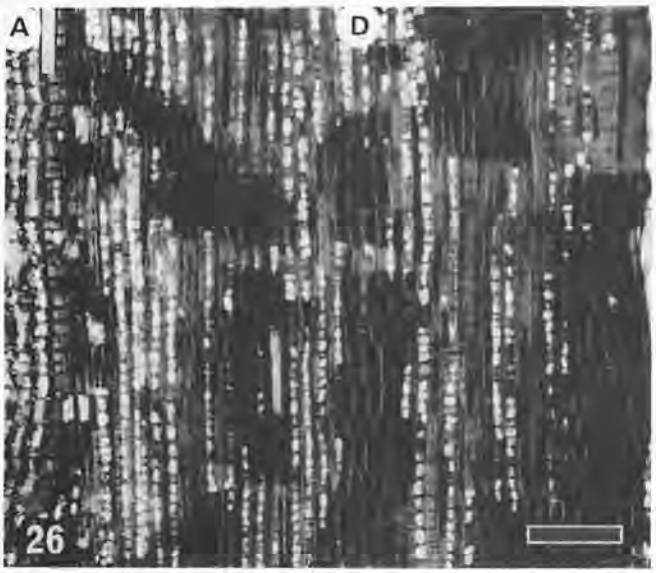
periderms cut off the old phloem before a necessity for dilatation adjustment arises. This phenomenon was already noted in other species by Holheide (1951). Dilatation in the mature bark is usually limited to a rather irregular symplastic tangential expansion and limited anticlinal division of axial phloem and ray parenchyma cells in the non-conducting phloem. A pseudocortex is never present (Figures 14, 16 & 26). In the dilatation zone some of the rays become distorted and their course is obscured by the dilatation growth. A regular funnel-shaped dilatation formed by proliferation of adjacent rays and mainly intervening axial phloem parenchyma was sporadically present in some samples of *E. zuluensis* (Figure 27). These wedges lack special dilatation meristems (reported by Chattaway 1955e in some *Eucalyptus* species) and could be seen with the unaided eye as cream coloured wedges on the transverse surface of dried bark samples (Figure 16E & F). Their presence seems to be diagnostic for the species.

In Myrtaceae, dilatation limited to axial phloem parenchyma was recorded in *Eucalyptus* (Chattaway 1953, 1955d & e), *Melaleuca* L. and *Syncarpia* Tenore. (Bamber 1962). An irregular and often slight dilatation of rays was observed in two South American species of *Eugenia* (Roth 1981). No previous reports of the presence of a pseudocortex in Myrtaceae could be traced. According to Roth (1981) little or no dilatation is expected in barks which shed their rhytidome every year. This statement seems to hold for the southern African species of *Eugenia* where the rhytidome in bark type Y is more frequently shed than in bark type X. Roth (1981) also suggests that the lack of dilatation growth in six other species of Myrtaceae studied by her is very possibly connected with the small bark width (2 – 5 mm diam.) of the species. The validity of this suggestion is debatable. Despite the pronounced dilatation growth in bark type X and frequent lack of it in bark type Y, bark diameter is rather similar (2 – 5 mm) in all the southern African species of *Eugenia*.

(e) Crystals

Crystals of calcium oxalate are very common in the secondary phloem of angiosperms (Zahur 1959; Esau 1969; Parameswaran & Liese 1970; Roth 1981). The shape and distribution patterns of these crystals are often of taxonomic significance (Metcalfe 1983). However, prismatic crystals are so frequently found in bark that it is usually not taken into account for diagnostic purposes. A notable exception is the presence or





Figures 25 – 27 Morphology of dilatation tissue. **25.** Radial section of *Eugenia simii* (*Van Wyk 1270*) shown under polarized light (compare Figure 26) showing the phellem (A), well developed phelloderm (B), pseudocortex (C) and non-conducting phloem (D) — note presence of crystalliferous idioblasts and lack of chambered crystalliferous strands in C and the abundant presence of the latter in D. **26.** Radial section of *E. zuluensis* (*Van Wyk 2664*) shown under polarized light (compare Figure 25) showing phellem (A) and non-conducting phloem (D) — note absence of well defined phelloderm and pseudocortex and predominance of chambered crystalliferous strands. **27.** Transverse section of *E. zuluensis* (*Van Wyk 2663*) showing a wedge of dilatation tissue. Scale line = 150 µm.

absence of chambered crystalliferous strands ('Kristallkamerfasser'; septate crystal fibres; septate crystal strands) which occur relatively infrequently and are usually diagnostic for the distinction of species, genera and even entire families, including Myrtaceae (Roth 1981).

Probably, the most outstanding feature of the secondary phloem of the investigated species of *Eugenia* is the abundant presence of superimposed chambered crystalliferous strands (Figures 25 & 26). These long axial chains are distributed uniformly throughout the secondary phloem with the exception of the rays and some of the dilatation tissues (see below). They either occur randomly or, more frequently, are arranged in small groups or interrupted tangential layers often bordering fibre clusters (especially on their outer side).

Crystals are deposited in the chambers immediately after differentiation at the vascular cambium. According to Esau (1969) chambered crystalliferous cells develop from fusiform parenchyma cells subdivided by transverse septae (partitions) into chambers (compartments). However, several authors (e.g. Milanez 1942; Chang 1954) have claimed that the crystal strands are by origin crystal-containing parenchyma strands. In *Eugenia*, whole series of chambers seem to be enclosed in a common wall because they do not separate during maceration. The strands are therefore considered to be composed of true 'chambered crystalliferous cells' in the sense of the IAWA Committee (1964). Crystalliferous chambers in the wood of *Eugenia* often separate during similar treatment (Van Wyk *et al.* 1983).

The cell walls and septae of the crystalliferous strands in the phloem are always thin and remain non-lignified. This is the case even with strands which are so closely intermingled or contiguous with phloem fibres that pressure owing to cell expansion often causes crystal-shaped impressions in the fibre walls. In this connection Parameswaran & Schultze (1974) have found, in *Acacia senegal* (L.) Willd., that those parts of the walls of the crystalliferous cells which are in immediate contact with the phloem fibres become thickened and lignified. Unlike those in bark, the crystalliferous chambers in the wood of *Eugenia* are nearly always sclerified (Van Wyk *et al.* 1983).

The crystalliferous chambers in the bark of the southern African species of *Eugenia* are usually more or less axially elongated and much smaller than the surrounding phloem parenchyma cells. Tanniniferous substances are absent from the strands. Each chamber contains a solitary prismatic crystal which is slightly longer than wide and therefore usually axially orientated. In contrast to those in the wood (Van Wyk *et al.* 1983), these crystals are apparently not surrounded by a distinct cellulosic sheath. The outline of the crystals usually differs in longitudinal and transverse sections (Figure 36) and seems to correspond to the twinned type ('Zwillingskristall' *cf.* Brögli 1926; Holheide 1951). A precise terminology to distinguish between different forms of prismatic crystals is desired since the shape (and size) of these crystals in the wood of *Eugenia* differs from that in the phloem (Van Wyk *et al.* 1983). The determination of the exact crystallographic forms of the crystals appears to be difficult and too cumbersome for routine comparative studies (Wallis 1951). Crystal shape may be related to the hydration form of the calcium oxalate (Pobeguin 1943; Franceschi & Horner 1980).

In Myrtaceae the main crystal type(s) deposited in the chambered cells of the phloem varies and is usually of considerable diagnostic importance (Chattaway 1959; Bamber 1962). Crystal type also features prominently in keys to the bark of various species of Myrtaceae presented by Brögli (1926) and Bamber (1962). All the species of *Eugenia s.str.* studied by Chattaway (1959) were characterized by the presence of twinned or rarely multiple crystals, but never druses. In *Syzygium s.l.* the crystals were mainly druses, only rarely solitary or in multiples.

In addition to the chambered crystalliferous strands, single more or less isodiametric thin-walled cells containing a druse, prismatic or rarely multiple crystals were sporadically present in the bark of all the investigated species. I refer to these cells as crystalliferous idioblasts although they are about the same size as the surrounding axial parenchyma cells. The crystalliferous idioblasts are derived from axial parenchyma cells and are usually confined to the non-conducting phloem and dilatation zones. Druse crystals were observed only in bark type X and predominate in the idioblasts of the pseudocortex (Figure 25), thereby contributing towards its possible confusion with the true cortex in which similar idioblasts occur (Van Wyk 1978). They are rather weakly assembled and bear some resemblance to star crystals or 'Morgensterndrusen' of German authors (Metcalfe 1983). The multiple crystals (small prisms) could be an artifact caused by the disruption of a druse or prismatic crystal during sectioning.

When transverse surfaces of dried bark samples (smoothed and covered with a layer of water or glycerol) are viewed under low magnification (e.g. ×10, hand lens), the numerous crystals in the chambered strands can often clearly be seen as regularly dispersed white grains. However, a striking feature of bark type X is the paucity of crystals in the outer zone of the inner bark. This zone is usually rather sharply demarcated from the inner, more crystalliferous part of the bark and corresponds to the pseudocortex (see 2d). Chambered crystalliferous strands were difficult to find in this tissue with the light microscope (Figure 25). What appears to be obliterated remains of strands have occasionally been observed. The crystals are apparently resorbed towards the outer bark and redeposited as larger druse crystals in the idioblasts (Figure 25). Bamber (1962) observed the disappearance (but not redeposition) of crystals in the non-conducting phloem of some Leptospermoideae. He suggested that this resorption could be a mechanism allowing the conservation of calcium in the phloem before loss into the rhytidome. The tendency for crystals to disappear after they have been formed was also observed by other authors in different taxa (see Metcalfe 1983 for references). Schimper (1886) according to Metcalfe (1983) cites an example in which calcium oxalate in leaves of *Crataegus monogyna* L. is first deposited as druses in the assimilatory tissue of the leaf. These subsequently disappear, but calcium oxalate is then again deposited in the form of prisms around the vascular bundles.

No resorption of crystals was apparent in bark type Y (Figure 26) and crystalliferous strands were still abundantly present in the non-conducting phloem cut off by deep-seated periderms. Strangely, no resorption of crystals was noticed in actively scaling samples of bark type X (notably *E. umtamvunensis*). Sequential periderm formation is very rapid in these samples and no pseudocortex develops. Could the paucity of crystalliferous strands and phloem fibres in the pseudocortex not perhaps be an indication that it is after all still the true cortex? This issue is discussed in more detail under 2d.

(f) Periderm

In the mature bark the pattern of periderm initiation determines, to a large extent, the structure of the rhytidome and eventually the bark surface pattern (see 2g). In addition, structural peculiarities of the periderm itself often supply excellent diagnostic characters (Roth 1981) and will subse-

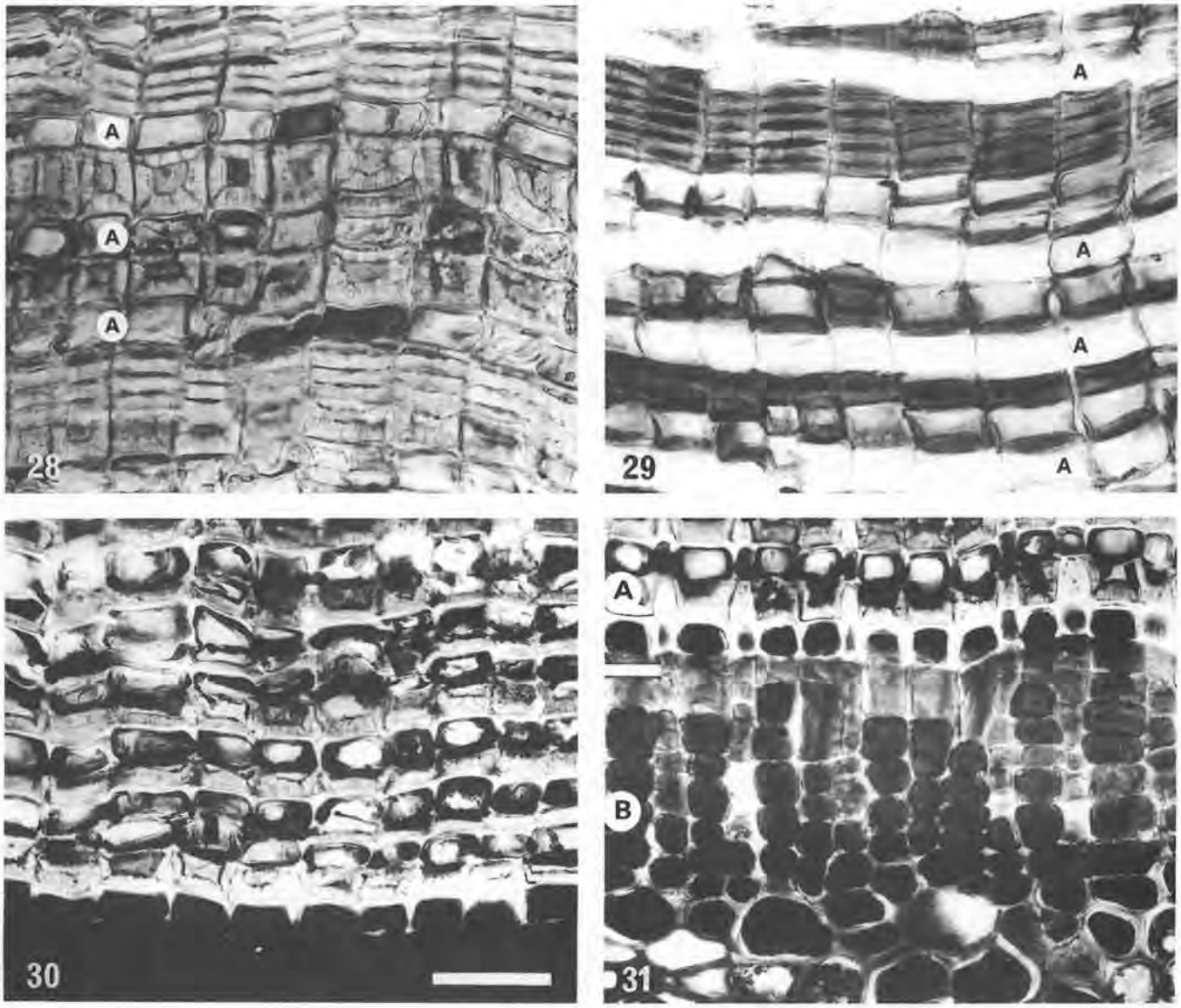
quently be considered in more detail.

The phellem in Myrtaceae is often stratified, thereby increasing the possibility of structural variation which may be considered for diagnostic purposes (Lignier 1886/87, 1890; Solereder 1908; Metcalfe & Chalk 1950). In southern African species of *Eugenia* structural details of the first-formed stem periderm have already yielded excellent diagnostic characters (summarized in Table 1) for the identification of species group X and Y (Van Wyk *et al.* 1980).

E. capensis differs from the species with bark type X in having relatively thick (1,0 – 2,5 mm) and predominantly cream coloured phellem (Figure 15c). The phellem is 0,3 – 0,6(0,8) mm thick and pinkish or reddish-brown in the remaining species of this group (Figure 15A, B, D & E). Maximum thickness of the phellem is rather uniform in mature samples of bark type Y and nearly always varies from 0,5 – 0,8 mm (Figure 16). It is cream coloured in transverse sections of dried bark samples.

Two types of phelloid cells are distinguished in the phellem. Phelloids with persistent wall thickenings (p-phelloids) were recorded in both types of bark (Figures 28 – 31 & 33) whereas cells with either unthickened walls or non-persistent thickenings (n-phelloids) were found only in bark type Y (Figures 32 – 35). For more differences between the two types of phelloids see 1a & b. Van Wyk *et al.* (1980) did not observe p-phelloids in the first-formed periderm of species group Y. Otherwise wall construction of phelloid and phellem cells is similar in the young and mature bark. However, differences in the radial diameter of the phelloid and phellem cell layers reported in the last article (compare Table 1) are not always so obvious in the mature bark. The chemical basis for the distinction between the two types of phelloid walls still needs clarification.

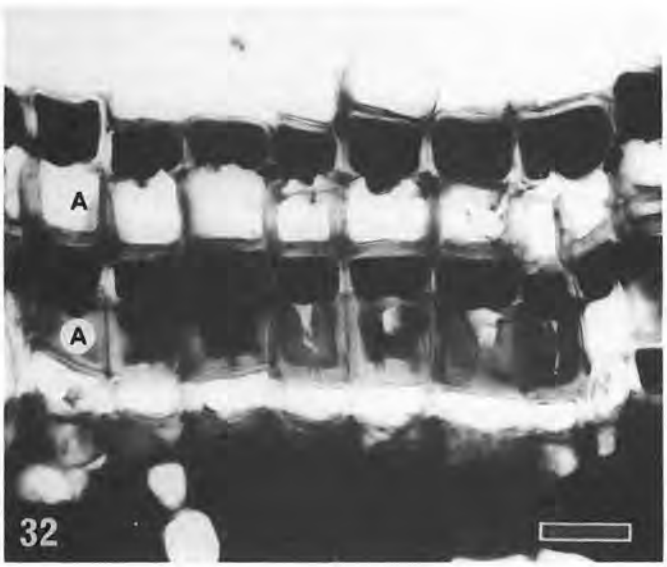
The p-phelloid layers in bark type X may be uniseriate (often in *E. natalitia*) (Figure 30) or up to ten cells wide with the multilayered parts tending to taper in short arcs (conspicuous and more or less continuous in *E. capensis*) (Figures 28 & 29). The frequency of p-phelloids is very variable in bark type Y and the multilayered arcs (especially conspicuous in *E. zeyheri* and *Eugenia* sp.A) are rarely more than six cells wide (Figure 33). Both types of phelloids may be found in the same cell layer, mixed in various proportions and varying from sample to sample.

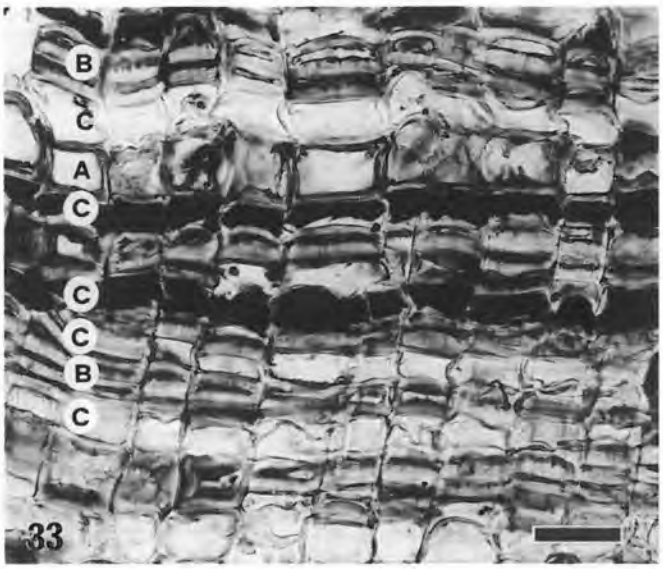


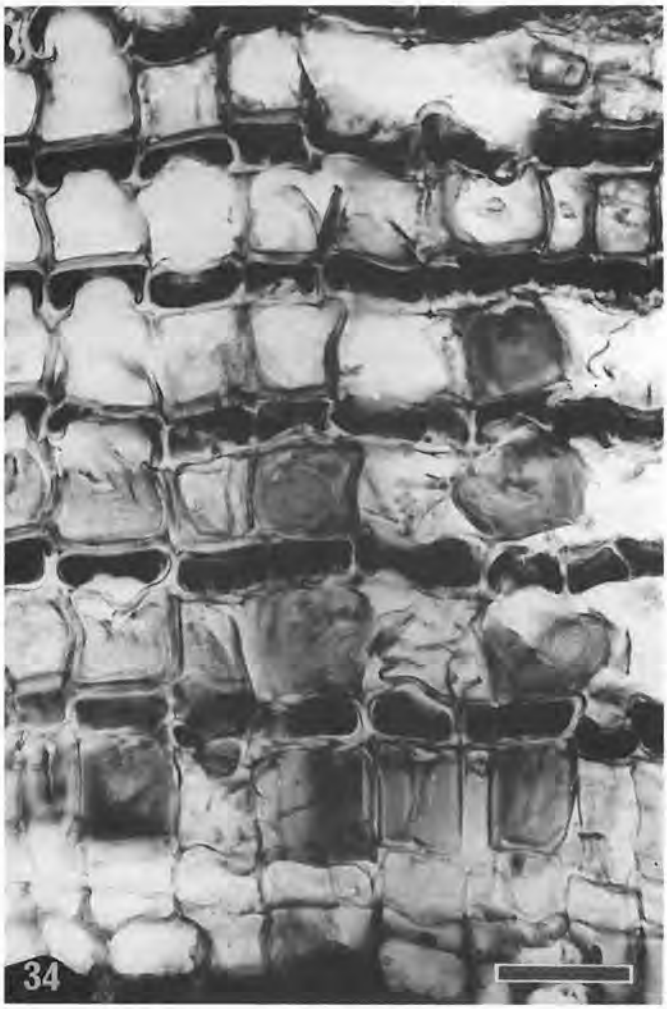
Figures 28 – 31 Periderm construction of bark type X. **28 & 29.** Transverse sections of *Eugenia capensis* (*Van Wyk 4508 & 4507*, respectively) showing uniserial layers of phellem cells (A) alternating with layers of thick-walled phelloid cells of variable thickness. **30.** *E. natalitia* (*Van Wyk 4252*), transverse section showing regular alternation of uniserial phellem cell layers (thin-walled and tanniniferous) with phelloid cell layers (thick-walled). **31.** *E. natalitia* (*Van Wyk 4252*), radial section showing phellem (A) and parenchymatous phelloderm (B) which merges with the pseudocortex. Scale line = 50 µm.

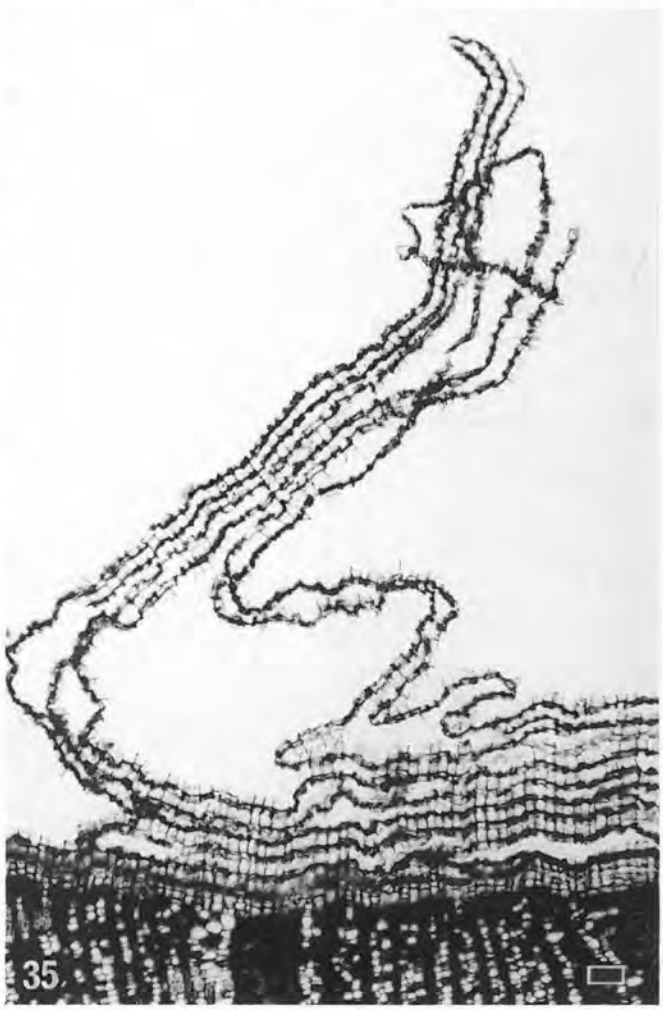
p-Phelloids were absent in all samples of *E. zuluensis* (Figure 35). Uniseriate layers of n-phelloids alternate with uniseriate layers of phellem cells to form a very regular phellem. Wall thickenings disappear very soon (usually already absent in the second phelloid layer from the phellogen) and subsequent fracturing of the radial walls allows the phellem cell layers to separate (Figure 35). These exfoliating papery sheets (pseudorhytidome) are a distinctive feature in *E. zuluensis* (see 2g).

The ease with which the phellem cell layers separate is









Figures 32 – 35 Periderm construction of bark type Y. Transverse sections. **32.** *Eugenia verdoorniae* (*Van Wyk 2335*) showing n-phelloids (A) alternating with strongly tanniniferous phellem cell layers. **33.** *E. woodii* (*Van Wyk 4061*) showing uniserial layers of phellem cells (C) alternating with layers of p-phelloids (B) and one clearly defined layer of n-phelloids (A — note some wall thickenings breaking up). **34.** *E. woodii* (*Van Wyk 2659*) showing uniserial layers of tanniniferous phellem cells alternating with uniserial layers of n-phelloids — wall thickenings lacking in older layers of phelloids. **35.** *E. zuluensis* (*Van Wyk 2664*) showing the separation of phellem cell layers owing to the disruption of radial cell walls in the layers of n-phelloids. Scale line = 30 μm.

apparently linked to the frequency of p-phelloids in the phellem. This phenomenon is, for example, absent or weakly developed in samples with an abundance of p-phelloids (always in bark type X). Samples of bark type Y, with very few of these cells, frequently display separation of phellem layers especially at the margins of periderm flakes (but never as conspicuous as in *E. zuluensis* where p-phelloids are absent).

A well developed phelloderm only occurs in bark type X (Figures 25 & 31). Up to ten layers of radially arranged cells, clearly belonging to the phelloderm, were recorded. The phelloderm cells are thin-walled and strongly tanniniferous. They merge gradually into the pseudocortex without any obvious distinction between the older cells of the two tissues. No conspicuous phelloderm was observed in the first-formed stem periderm (Van Wyk *et al.* 1980).

Chattaway (1959) recorded a number of differences between the barks of *Eugenia s.str.* (mainly New World species) and *Syzygium s.l.* Bark type X agrees with the bark of the former group in the composition of the phellem and presence of a phelloderm with unthickened cell walls. Bark type Y also agrees with the general periderm pattern of the New World species of *Eugenia* (Chattaway 1959; Roth 1981). However, an evaluation of the taxonomic significance of the two types of phelloid cells in bark type Y does not seem to be possible at this stage owing to a lack of comparative data. As far as I have ascertained, no similar distinction between phelloid cells has yet been recorded in *Eugenia s.str.* There is a need for more detailed information on the structure of the periderm in other Old World species of *Eugenia s.str.*

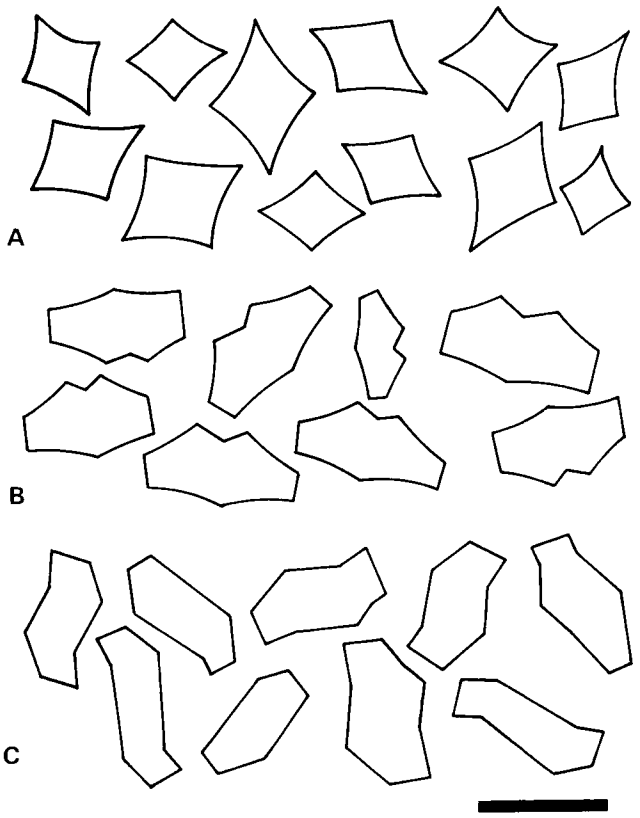


Figure 36A – C Shape and size of calcium oxalate crystals from chambered crystalliferous strands in the bark of various southern African species of *Eugenia*. **A.** Shape most frequently seen in transverse sections of bark and representing polar views of B & C. **B & C.** Two variations of crystal type most frequently seen in radial and tangential sections. Scale line = 20 µm.

(g) Rhytidome, sloughing and surface pattern

The visual impression of the bark surface from a distance may be sufficiently distinct for instant recognition of many tree species. Bark surface characters are frequently used as the initial division in keys identifying trees by their bark (Beard 1944; Wood 1952). Bark types X and Y may be distinguished on the basis of bark surface pattern alone. This is an extremely useful aid for field recognition of forest species especially. The flaky surface pattern in bark type Y (Figures 7 – 12) is particularly conspicuous and has in fact long been used to identify *E. zuluensis* in the forests of Natal. The surface pattern in bark type X (Figures 1 – 6) is either rather smooth or weakly dippled-scaly (in short referred to as dippled). The latter term was among others employed by Corner (1940), Henderson (1949) and Whitmore (1962a, b & c, 1963) and alludes to the shallow more or less circular depressions left on the bark by the desquamating scales. Thorenaar (1926) used the comparable term 'pokdalig' and on the basis of scale size distinguished between 'grof pokdalig' and 'fijn pokdalig'. The formation and sloughing of scales is a cyclical process. Different parts of the bole, often in zones, are commonly out of phase. This is especially noticeable in some species with dippled bark (Figure 5). It should also be stressed that the distinction between type X and Y bark surfaces is only reliable if the mature bole bark is considered.

Bark surface patterns are the result of the interactions between rhytidome, sloughing pattern and external weathering processes (Whitmore 1962a). Differences in surface configuration between bark types X and Y can be explained mainly by the details of the specific sloughing patterns involved. Sloughing patterns can be analysed into the distribution, texture, shape and size of the scales and whether they are loose hanging or adhering before sloughing (Whitmore 1962a). These patterns (see Figure 14) should be carefully compared because actively sloughing samples of bark type X may be mistaken for type Y (the former type is after all only a kind of 'flaky' bark). Scales in type X are occasionally irregular in outline thereby increasing the chance of confusion. On the other hand local parts of bark type Y may be fairly smooth at times, especially after rapid sloughing of relatively large pieces of rhytidome (often in *Eugenia* sp.A). However, there will nearly always still be at least one sheet-like rhytidome layer present (Figure 16) whereas smooth areas in bark type X are usually characterized by a single superficial periderm and no dead inner bark tissue (Figure 15A – C). A useful 'field character' to distinguish scaly samples of bark type X from type Y is to determine the structure of the scales (compare Figure 14).

The bark surface pattern in *E. capensis* is rather smooth, finely fissured and usually without conspicuous scales (Figure 1). It is clearly distinct among the species with bark type X. The single superficial periderm is maintained for a long time. A relatively thick phellem develops (see 2f) and its outer layers are slowly weathered away as tiny inconspicuous lamellas. The bark surface is sculptured by fine vertical and occasionally transverse fissures. These are superficial and limited to the phellem only (Figure 15C).

Although a conspicuous rhytidome is absent, *E. capensis* does slough tiny inconspicuous scales which slowly erode the cortex and later the pseudocortex. Conspicuous scales were found only once in a tree with an exceptionally thick bole. There is little doubt that what has been taken for the mature bark pattern in this species could still alter in very old trees. However, it is the bark pattern nearly always encountered in the field and, therefore, the most meaningful one to use for

species recognition.

Bark surface patterns are rather similar in *E. natalitia* (Figures 4 – 6), *E. simii* (Figure 2) and *E. umtamvunensis* (Figure 3). The surface, nevertheless, tends to be smooth more frequently with relatively few scales in the first two species. Scales are usually present on most parts of the bole in *E. umtamvunensis*. In all these species the periderm is maintained for a long time (as in *E. capensis*) but the phellem is much thinner than in the last species. Fine vertical and, more rarely, transverse fissures are usually restricted to the phellem (often obscured by the growth of microlichens) — occasionally forming a rather regular grid-cracked pattern.

The structure of the scales and the way they are sloughed are very distinctive in bark type X. Each scale constitutes one rhytidome layer (called layer-thick scales by Whitmore 1962a) sloughed down to the new periderm and shed as a discrete unit (Figure 14). The dimensions of the scales are therefore mainly determined by the successive more deeply seated periderms. In one sample of *E. umtamvunensis* most scales had one or more additional anastomosing periderms forming an integral part of the scale (Figure 15D). More samples of *E. umtamvunensis* should be studied to ascertain whether this unusual structure occurs frequently in the species, or is an anomalous condition.

The plane of sloughing of the layer-thick scales is within the outer phellem layers of the periderm responsible for cutting off the scale (Figure 14). The new surface is slightly powdery, and, with the colour of the phellem, usually reddish-brown (Figure 3). Broken-off ends of fibres penetrating the periderm are usually present. This way of sloughing is allegedly caused by the expansion and contraction of the rhytidome as a result of fluctuating moisture content and probably also further increase in the girth of the stem (Thorenaar 1926). Rapid shedding of the scales is usually enhanced by the presence of phelloid layers in the phellem — as in *Eugenia*. These constitute layers of weakness and are ruptured during the differential movement of the tissue (Von Höhnel 1877 according to Thorenaar 1926, pp. 27 & 28).

Once the inner bark tissue has been cut off by a periderm it becomes blackish-brown and very firm in bark type X. Scales are shed with the cut-off tissue still intact and this suggests an apparent resistance to decay. The phellem (at least the phellem cells) is rather resistant to decay. It seals off the scales (except for fissures and cracks) and may to some extent protect the inside of the scales against weathering and insects, bacteria and fungi which may cause decay. It may also be that the scales do not remain on the bole long enough for decay and mechanical erosion to cause noticeable rotting.

In bark type Y the successive periderms remain coherent and the shedding of the scales as described for type X is not possible. Up to eight (rarely more) rhytidome layers may be present, each usually between 0,5 – 2 mm thick (Figures 14 & 16). The tissue cut off from the inner bark dies, alters in colour and starts to decay. Decayed tissue is gradually eroded away, especially by rain water, leaving only the more resistant periderm layers (Figure 13). The only way the dead rhytidome tissues can adjust to tangential strain, is by splitting apart. There is no dilatation of parenchyma in the rhytidome as reported in some Leptospermoideae (Chattaway 1953; Bamber 1962). Because of the thickness of the rhytidome, fissures can be quite conspicuous and may cut through several rhytidome layers. Fissuring supplemented by weathering results in the progressive break-up of the periderm system into flakes. No definite sloughing mechanism is present and the shedding of the irregularly outlined, loose-hanging flakes of periderm is mainly determined by external weathering processes. Newly exposed periderm layers are covered by remnants of dead phloem tissue but these are often completely weathered away by the time they are sloughed (Figures 13, 14 & 16).

In *E. zuluensis* the cut-off phloem tissue usually becomes pale yellowish-brown — unlike the dark blackish-brown of the other species. It also tends to decay more rapidly leaving a bloom of powdery yellowish or brownish material on the periderm. I suspect that the intensity of the colour change is to some extent influenced by the tannin content of the dead phloem tissue. Although tanniniferous cells do occur in the secondary phloem of *E. zuluensis* (see 2a), previous studies have clearly shown that this species is less tanniniferous than the other southern African species of *Eugenia* (Van Wyk 1978; Van Wyk *et al.* 1983).

E. zuluensis also differs from all other investigated species by the sloughing (in addition to the flakes of periderm) of conspicuous thin papery sheets consisting only of a layer of phellem cells with phelloid remnants on both surfaces. These sheets have often curled up at the edges. The fracturing of the phelloid cell walls in the stratified phloem is responsible for the peeling of these layers of phellem cells (Figure 35). Exfoliating layers of a stratified periderm are called a pseudo-rhytidome by Roth (1981, p.120). In the other species of *Eugenia*, separation of the phellem cell layers is nearly always inconspicuous and confined to the edges of periderm flakes.

With the exception of *E. zuluensis*, separation of individual species of group Y on the basis of bark surface pattern unfortunately does not appear possible. Although bark type Y is characterized by a more substantial rhytidome than type X, it is very variable in thickness and surface pattern even on one tree. Rhytidome layers continuously develop and slough so that the number present varies. This variation between individuals, as a result of the cyclical development and sloughing of rhytidome layers, is common in scaly barks (Whitmore 1962a).

The rhytidome also tends to be relatively thick and flaky in *E. zeyheri* and *Eugenia* sp.B but thin and smoother in *Eugenia* sp.A. External weathering seems to play a major part in controlling the size, shape and abundance of the flakes. The rhytidome shows variations in, particularly, the degree of rotting and deciduousness of the scales which perhaps depends mainly on the microclimate around the tree. Variation in the bark often occurs in trees from open and forest habitats. The rhytidome of trees found in the open or forest margin tends to be thicker with more rhytidome layers present. The thicker layers of dead tissue are subjected to stronger fissuring forces and desiccation is greater than within the forest. Rotting is also slowed down by the drier conditions and the loose-hanging flakes of periderm are not so readily shed. The bark therefore becomes more strongly fissured with a more flaky aspect.

The colour of the bark surface varies from almost white to various shades of grey in the investigated species. Bark type Y is often easily recognized by the bloom of superficial dark brown or black (rarely bleached to almost white) dead phloem tissue on the flakes of periderm (Figure 13). Non-vascular epiphytes are abundantly present on the bark surface — especially in forest species. White or grey patches of microlichens are characteristic in bark type X (not so frequent in *E. capensis*) (Figures 1 – 6). Boles flecked with microlichens are often a feature of the smooth barks in slow growing trees with long persistent surfaces (Whitmore 1962a, b & c; Roth 1981) and may be so specific as to aid the recognition of particular species in the forest (Whitmore 1975). Boles with

bark type Y (particularly *Eugenia* sp.A) are occasionally mottled with whitish flecks but these are usually caused by a fungus belonging to the Basidiomycotina and not by microlichens (Figure 9).

(h) Slash

Of the many features of the slash (blaze, bark section) which may be described (Wood 1952), only bark width and inner bark colour will be considered. Notes on the colour of the periderm and phloem tissue in the rhytidome are supplied elsewhere in this article.

Total bark width (inner bark plus rhytidome) is influenced by the rate at which the rhytidome sloughs at the surface. This applies particularly to bark type Y which is characterized by a more substantial rhytidome of which the thickness depends to some extent on the intensity of weathering (Figure 16). Total bark thickness in bark type X also differs substantially before and after the shedding of scales. Rhytidome width is usually in the range of (1,0)1,5 – 2,5(4,0) mm in bark type Y and 1,0 – 3,0 mm in type X.

The inner bark of mature trees has a roughly constant thickness and is, therefore, more reliable for comparative purposes. It is nearly always in the range (0,6)1,0 – 2,0(3,5) mm in bark type Y. No significant interspecific differences were noticed in this group (Figure 16). A striking feature is supplied by the large inner bark width, (3)5 – 8(10) mm, in *E. umtamvunensis* (Figure 15D). In the remaining species of group X the inner bark is relatively thin, varying from (0,8)1,0 to 2,0(2,5) mm (Figure 15A – C). In a study of tropical American barks Roth (1981) found that the occurrence of a very thin bark (1 – 3 mm) was rare, recording it in only a few families, notably, Rubiaceae, Melastomataceae and Myrtaceae (Myrtoideae).

If the rhytidome (or periderm) is scraped off to expose the outer edge of the inner bark, a greenish zone of tissue usually becomes apparent in bark type X. It is caused by greenish pigment (chlorophyll?) in the plastids of the pseudocortex (including phelloderm) and adjacent parts of the phloem rays. It may be absent in those parts of the bark where active scaling occurs. The green zone in young stems of this group, however, corresponds to the primary cortex and outer part of the secondary phloem. A green zone is nearly always absent in mature samples of bark type Y (which lacks a well defined phelloderm and pseudocortex), although it is usually present in young bark where the pigment is contained in the outer part of the phloem rays which may be dilated.

Roth (1981) also found a green layer in the bark of some tropical American species of Myrtoideae. In most cases she interpreted a green zone beneath the cork layer as a phelloderm. However, the soundness of this assumption is questionable in view of the aforementioned observations of the present study.

The freshly cut inner bark is nearly always either pinkish-brown or light brown in the species studied. It was therefore surprising to find a striking dark reddish-brown inner bark in *E. umtamvunensis*. Unfortunately, only a limited number of trees with mature bark are known at present. It would be interesting to see whether this character will hold, should more large trees be discovered. Incidentally, one of the characters used by Van Wyk (1982) to separate *E. umtamvunensis* from *E. natalitia* is the darker rusty brown bark surface on new branchlets of the former species.

3. Bark types X and Y in relation to phloem growth rate

Whitmore (1962b) formulated a number of principles to account for bark construction in the Dipterocarpaceae. These principles were subsequently employed to explain different bark patterns in Fagaceae (Whitmore 1963). Phloem growth rate in particular was shown to be an important factor for the interpretation of bark surface patterns. The present study has revealed patterns of bark construction in *Eugenia* comparable to bark types in the first two families. The extent to which a similar analysis could be applied to suggest possible control of the two main types of bark surface pattern in the *Eugenia* species studied, will be considered here.

Whitmore (1962b) deduced, from indirect calculations, that the tangential extent of the dilatation tissue at a given distance from the vascular cambium in any bark is a direct measure of the total amount of accommodation of strain and hence the relative growth rates of xylem and phloem at the cambium. It was in fact shown that the tangential strain, and hence the xylem/phloem ratio, is the highest in barks with a pseudocortex (dilatation tissue more than 70% in extent at the inner bark surface) while a relatively low xylem/phloem ratio is present in bark types in which tangential growth is slight (dilatation tissue less than 30% in extent at the inner bark surface or entirely symplastic). Whitmore (1962b) also demonstrated that the xylem/phloem ratio is inversely proportional to the phloem growth rate since the different groups of dipterocarps studied have similar xylem growth rates. It follows, therefore, that the phloem growth rate is fast in bark with a low xylem/phloem ratio, but slow in bark where this ratio is high. This means that phloem growth rate may be indirectly estimated from the amount of dilatation tissue formed. It also implies that if bark thickness remains constant, sloughing rate must be proportional to phloem growth rate. Whitmore (1962b, 1963) found that scaly bark is characterized by little dilatation tissue and a fast phloem growth rate, whereas smooth or dippled bark has a pseudocortex and a slow phloem growth rate. He, therefore, suggests that phloem growth rate is an important factor in the control and evolution of bark surface patterns in Dipterocarpaceae and Fagaceae.

The mature inner bark of *Eugenia* remains about the same thickness (see 2h). It is reasonable to conclude that it is sloughing at the rate at which it forms. Xylem growth rate appears to be approximately similar [average (0,6)0,8 – 1,0(1,4) mm per growth ring] in all the species, judging from the average width of the growth rings in the wood (assuming that each ring represents an annual increment). Unfortunately the growth rings were often very indistinct or obviously smaller than a single annual increment and therefore not very reliable for detailed calculations.

Bark type X is characterized by a pseudocortex and a smooth or dippled bark surface. It is suggested that the xylem/phloem ratio is high in these barks and that the phloem grows slowly and the rhytidome forms and sloughs slowly. Conspicuous patches of microlichens commonly occur on bark type X, suggesting that it is indeed a slowly growing and slowly sloughing bark. Whitmore (1962b) considered a dippled bark to be intermediate between smooth and scaly bark types. He also found that the formation of a dippled bark in Dipterocarpaceae is favoured by the presence of a pseudocortex.

Bark type Y is characterized by relatively little dilatation growth in the inner bark and a flaky bark surface. It is suggested that these barks have a low xylem/phloem ratio and therefore a fast phloem growth rate and sloughing rate. Microlichen patches are usually absent or relatively small, suggesting that the sloughing rate is higher than in bark type X.

It should be instructive if the indirect method of calculating

phloem growth rate, which was developed by Whitmore (1962b, 1963), could be supplemented by more direct measurements of cambial activity. Radiological methods such as the autoradiographic technique proposed by Waisel & Fahn (1965) may suit this purpose. Waisel *et al.* (1966) used this method on saplings of *Eucalyptus camaldulensis* Dehn., and found that the number of xylem layers produced to the number of phloem layers produced (4:1) is practically independent of many environmental factors.

It is known that the first-formed stem periderm arises subepidermally in the cortex and to the inside of the extraxylary fibre cylinder in bark types X and Y, respectively (Van Wyk *et al.* 1980). In view of the causal relationship between phloem growth rate and periderm pattern, suggested by Whitmore (1962b) and now applied to *Eugenia* bark, the question arises as to whether the site of periderm initiation (superficially *vs.* deep seated) in the young stem may be an indication of xylem/phloem ratio.

Taxonomic conclusions

Bark features of the *Eugenia* species studied agree with the bark anatomical descriptions for Myrtaceae in general and *Eugenia s.str.* of the New World in particular. A meaningful comparison with bark features of other Old World species of *Eugenia s.str.* was not possible owing to a lack of comparative data.

A previous division of the southern African species of *Eugenia* into two supraspecific groups, X and Y, is paralleled by the structure of the mature bark. Bark types X and Y are distinguished as two general categories named after their respective species groups. This lends further support to the view that the two groups of species represent a natural subdivision of *Eugenia* in southern Africa.

Among species with bark type X, *E. capensis* and *E. umtamvunensis* may be told apart by slight variations of the general bark type. Bark construction is rather similar in *E. natalitia* and *E. simii*, although sufficiently distinct from the first two species. More bark samples of *E. umtamvunensis* need to be studied because of the paucity of material available in the present study (diagnostic characters summerized in Table 4).

Efforts to distinguish between species with bark type Y on the basis of bark differences were not very successful. Of the eight species studied, only *E. zuluensis* could readily be told apart (Table 5).

By inference from bark studies on other groups, it is suggested that phloem growth rate may be an important factor controlling differences in bark structure between types X and Y.

Features of the bark are far more useful than those of the wood to aid identification of species and elucidation of relationships.

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CHAPTER 8

MORPHOLOGY AND TAXONOMIC VALUE OF POLLEN

The genus *Eugenia* (Myrtaceae) in southern Africa: Morphology and taxonomic value of pollen

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The taxonomic significance of pollen morphology was assessed in 14 southern African species of *Eugenia* L. Up to now African species of *Eugenia* were considered to be androdioecious and therefore pollen from both male and hermaphrodite plants was compared. All the investigated species produce pronounced dimorphic pollen. Pollen from male flowers is typically myrtaceous and resembles that of consistently hermaphroditic species of *Eugenia* in other parts of the world. Grains are free, radially symmetrical, isopolar, oblate to peroblate, (17)20 – 25(30) µm in equatorial diameter, triangular, goniotreme and tricolporate. Pollen from hermaphrodite flowers deviates considerably from the typical myrtaceous pattern. Grains are free, radially symmetrical, apolar or heteropolar, spheroidal, (22)28 – 35(40) µm in diameter and atreme or colpate. The lack of ora (endopores) suggests that these grains are most probably inviable (or almost so), thus rendering the flowers functionally female. All the investigated species therefore appear to be functionally dioecious. It was impossible to differentiate between species on the basis of palynological features. Neither did pollen morphology reflect a recently proposed subdivision of *Eugenia* in southern Africa.
S. Afr. J. Bot. 1985, 51: 371 – 378

Die taksonomiese waarde van stuifmeelmorfologie is by 14 Suider-Afrikaanse *Eugenia* L.-spesies ondersoek. Tot nog toe is *Eugenia* in Afrika as androdiësies beskou en daarom is stuifmeel van beide manlike en tweeslagtige plante vergelyk. Uitgesproke dimorfiese stuifmeel word deur al die ondersoekte spesies geproduseer. Stuifmeel van manlike blomme is tipies Myrtaceae-agtig en stem met stuifmeel van die deurgaans tweeslagtige *Eugenia*-spesies in ander dele van die wêreld ooreen. Korrels is vry, radiaalsimmetries, isopolêr, oblaat tot peroblaat, (17)20 – 25(30) µm in ekwatoriale deursnee, driehoekig, goniotreem en trikolporaat. Stuifmeel van tweeslagtige blomme wyk opvallend van die tipiese Myrtaceae-patroon af. Korrels is vry, radiaalsimmetries, apolêr of heteropolêr, sferoïdaal, (22)28 – 35(40) µm in deursnee en atreem of kolpaat. Weens die afwesigheid van ora (endoporieë) word vermoed dat die korrels heel moontlik steriel (of so te sê steriel) is. Dit impliseer dat die blomme funksioneel vroulik is. Dit wil gevolglik voorkom asof die ondersoekte spesies funksioneel tweehuisig is. Dit is onmoontlik om op grond van palinologiese kenmerke tussen die spesies te onderskei. Die onlangs voorgestelde onderverdeling van *Eugenia* in Suider-Afrika word ook nie deur die stuifmeelmorfologie weerspieël nie.
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Keywords: Androdioecy, dioecy, *Eugenia*, Myrtaceae, pollen

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Introduction

The pollen morphology of Myrtaceae is fairly homogeneous and the family was considered by Erdtman (1952) to be stenopalynous. Subsequent studies have, however, revealed slight differences which make it possible to recognize certain genera or species (Pike 1956; McIntyre 1963; Gadek & Martin 1981; Patel *et al.* 1984).

Eugenia s.str. constitutes several hundred species largely confined to the New World tropics. Relatively few species occur in Africa and the rest of the Old World. Recent studies have shown that *Eugenia* in southern Africa can be subdivided into two co-ordinate supraspecific groups (tentatively referred to as groups X and Y) of perhaps generic status (for references see Van Wyk & Botha 1984). A peculiar feature of these southern African members is that all the species of both groups X and Y show sexual dimorphism. Plants are androdioecious, that is, some plants produce morphologically male and some morphologically hermaphrodite flowers. For *Eugenia* this condition has only been reported in African species (e.g. Amshoff 1958; White 1978).

For a real understanding of the taxonomy of *Eugenia* all types of evidence need to be considered. Unfortunately palynological observations on *Eugenia* in southern Africa are scanty. In a comprehensive survey of the pollen morphology of Myrtaceae, mainly from the south-west Pacific area, Pike (1956) only briefly summarized the characteristic pollen features of the southern African *E. albanensis* Sond. and *E. capensis* (Eckl. & Zeyh.) Sond.

This paper reports on a detailed study of the pollen morphology of *Eugenia* in southern Africa. Palynological data are considered with regard to the delimitation and definition of taxa — particularly the recently suggested supraspecific groupings. In addition, the morphology of pollen from both male and hermaphrodite flowers is compared.

Materials and Methods

The pollen of 14 southern African species of *Eugenia* was examined by light (LM) and scanning electron microscopy (SEM). Pollen from both hermaphrodite and male plants was considered. Species names and specimens examined are given in Table 1.

Polleniferous material was obtained from herbarium specimens and treated by the acetolysis method (Erdtman 1960). For LM the treated grains were mounted in glycerine jelly and the cover slips sealed with paraffin wax. For SEM the pollen was air-dried from distilled water and sputter-coated with gold.

Measurements of the equatorial diameter were made with

Table 1 Species of *Eugenia* studied and material examined. Unless otherwise indicated, all collection numbers are those of the first author and specimens are deposited in PRU

Species	Material examined	
	Male	Hermaphrodite
Group X		
E. capensis (Eckl. & Zeyh.) Sond.	2588; 2644	2586; 2589; 2643
E. cf. mossambicensis Engl.	2495; 2498	2494
E. natalitia Sond.	5988; *Hemm* 348	6852; *Ward* 5244 (PRE)
E. simii Duemmer	4173; 4176; 4178; 5767	4172; 4175; 4177; 4179
E. umtamvunensis Van Wyk	5133; 5134	5132
Group Y		
E. albanensis Sond.	3139; 3276	3140; *Abbott* 335
E. erythrophylla Strey	5287; *Abbott* 1462	*Van Wyk & Venter* 1312 & 1314
E. verdoorniae Van Wyk	6124; 6128	3280; *Abbott* 1016
E. woodii Duemmer	5578; *Müller* 3735	*Hemm* s.n.; *Müller* 3736
E. zeyheri (Harv.) Harv.	3126; 3129	2417; 6851
E. zuluensis Duemmer	3292; 3295	3291; 3294
E. sp. A	5075; 5077	5078; 5079
E. sp. B	4240; 4343	4239
E. sp. C	5096; 5104	5099; 5106

the aid of a projection LM and were usually based on at least 20 grains per sample. Only the range encountered is supplied in this paper. In nearly all the samples the oblate/peroblate shape of the pollen resulted in all the grains being orientated on the slides with one of the poles facing uppermost. This prevented the taking of accurate measurements of the polar diameter. Polar diameter measurements were made from SEM micrographs just to confirm the oblate/peroblate shape (grains are usually somewhat collapsed/contracted, rendering measurements from this source not very reliable for comparative purposes).

The descriptive terminology used follows mainly Erdtman (1969) and the attempts at standardization offered by Reitzma (1970) and Nilsson & Muller (1978). In some instances alternative terms, used in a similar context by previous authors in descriptions of Myrtaceae pollen, are supplied in square brackets. Descriptors to indicate abundancy and frequency are based on those proposed by Schmid (1982).

Results

All the investigated species of *Eugenia* produce dimorphic pollen. Pollen grains from male and hermaphrodite flowers are regularly differentiated on size, shape and aperture features. There are no constant features with which individual grains can be identified with certainty to species. Neither could we find any consistent palynological differences between species groups X and Y.

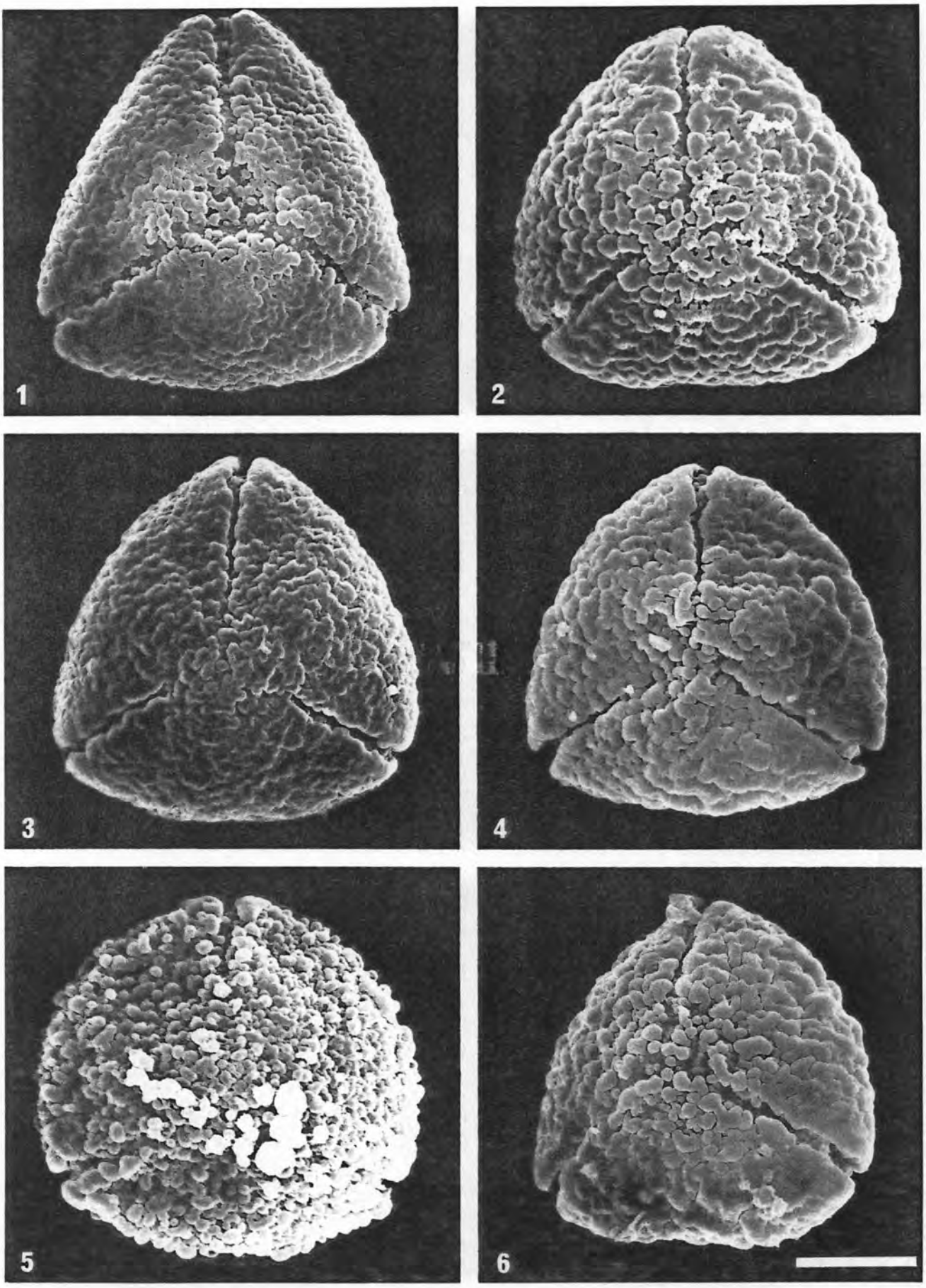
We shall refer to the pollen from male and hermaphrodite flowers as pollen types A and B, respectively. The morphology of pollen types A (Figures 1 – 12) and B (Figures 13 – 22) is separately described below. These general descriptions include the entire range of variability for all the investigated samples. Outstanding differences between the two types of pollen are summarized in Table 2.

Pollen type A (male flowers)

Pollen shed as monads. Grains radially symmetrical [radiosymmetrical], isopolar, oblate to peroblate, (17)20 – 25 (30) µm equatorial diameter. Amb triangular, sides of amb slightly convex or occasionally straight, angles obtuse [rounded], goniotreme [angulaperturate]. Grains tricolporate (very rarely di- or tetracolporate). Colpi [ectoapertures; meridional colpi] well defined, *ca.* 0,5 µm wide towards equatorial region, arcuate (when syncolpate), either longicolpate, syncolpate or tending to be parasyncolpate (but never with regularly shaped apocolpia). Ora [endoapertures; equatorial colpi; endocolpi] distinct, apparently lalongate. Vestibula nearly always apparent, up to 6 µm wide, 1 µm deep at apex. Exine 1 – 1,3 µm thick, sexine [ektexine *sensu* Faegri & Iversen (1950) but not (1964)] and nexine [endexine *sensu* Faegri & Iversen (1950) but not (1964)] of approximately equal thickness but occasionally not clearly distinguishable. Sexine pertectate,

Table 2 Summary of main morphological distinctions between pollen of male and hermaphrodite plants in *Eugenia*

Character	Male	Hermaphrodite
Polarity	Isopolar	Apolar or heteropolar
Size (equatorial diameter)	(17)20 – 25(30) µm	(22)28 – 35(40) µm
Shape	Oblate to peroblate	Spheroidal
Amb/outline	Triangular	Circular
Aperture type	Tricolporate	Atreme or colpate
Colpus pattern	Regularly longicolpate, syncolpate or tending to be parasyncolpate	Often anastomosing but without definite pattern; often with only one large ± circular colpus
Vestibula	Present	Absent
Exine thickness	1 – 1,3 µm	2 – 2,5 µm



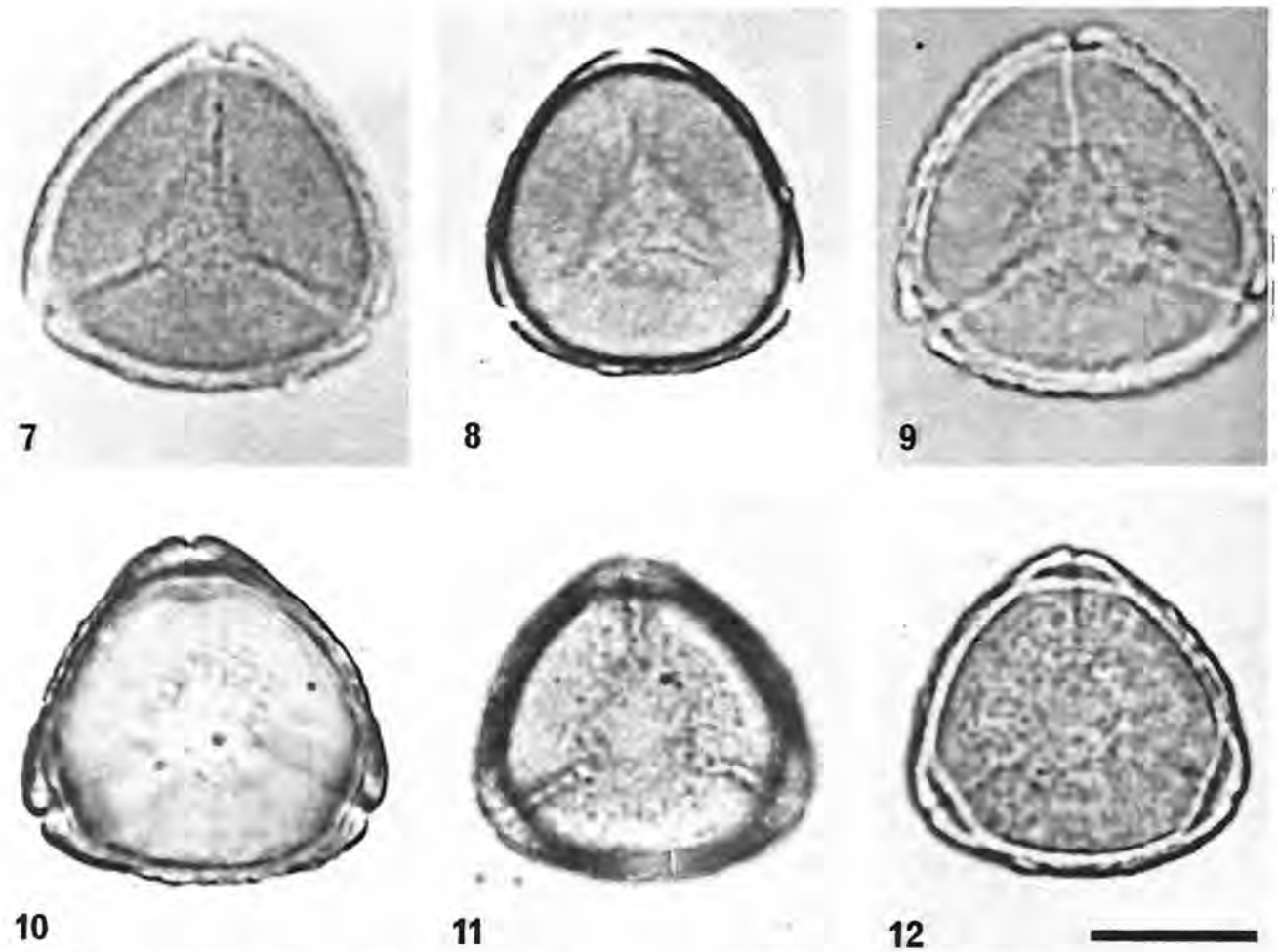
Figures 1–6 Pollen from male plants. SEM micrographs of grains in polar view. **1.** *E. umtamvunensis* (*Van Wyk 5133*). **2.** *E. zuluensis* (*Van Wyk 3295*). **3.** *E.* sp. A (*Van Wyk 5075*). **4.** *E. woodii* (*Van Wyk* 5578). **5.** *E. zeyheri* (*Van Wyk 3129*), the grains of this sample are rather atypical in having a more rounded amb and supratectal processes which tend to be clavate. **6.** *E.* sp. B (*Van Wyk 4240*), grain somewhat inclined. Scale line = 5 µm.

unstructured in optical section. Sexine surface with microscabrate, microrugulate, rugulate or very rarely microclavate sculpturing, occasionally with a narrow unsculptured zone bordering the colpi only in the equatorial area. Colpus membrane smooth or usually with scattered sexine elements (verrucae or gemmae), particularly in the area of colpal fusion in syncolpate grains. If these elements are densely packed the sculpturing of the latter areas resembles that of the mesocolpia and may be considered rudimentary apocolpia.

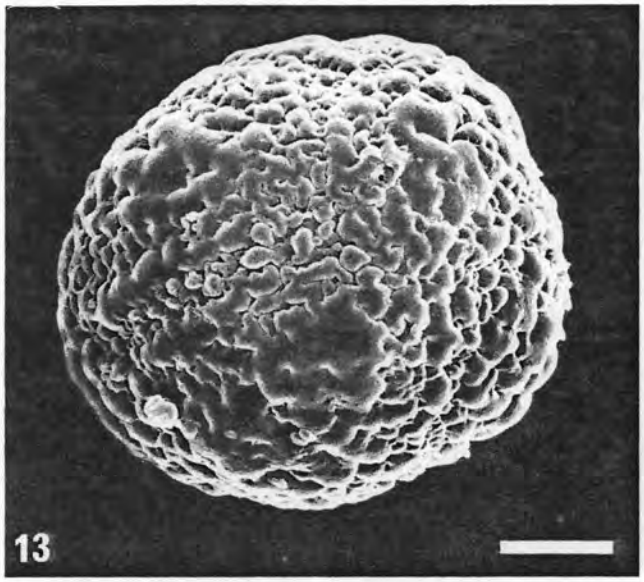
In pollen type A grain size, aperture number, shape of amb, apocolpal occurrence and sexine sculpture may show intraspecific variation. Grain size varies within fairly narrow limits (usually ± 3 µm, rarely up to 8 µm) within and between samples. The grains are nearly always tricolporate. Small numbers (± 1%) of di- and especially tetracolporate grains were occasionally present in some samples. Variation in the shape of the amb may be due to volume changes within the grain. More or less straight amb sides tend to be more frequent in samples from species group X. It is the feature most suggestive of a distinction between species groups X and Y, but unfortunately the considerable intraspecific variation renders this character taxonomically unreliable. The degree of fusion between the colpi in the polar region varies considerably both within and between samples. Usually the majority of grains in a sample are either syncolpate (Figures 1, 2 & 6) or longicolpate (Figures 3, 4, 5, 7 & 11) with at least some of the other type also being present. No true parasyncolpate grains were recorded. However, in syncolpate grains the colpus membrane over the poles is usually covered by verrucae or gemmae (Figures 1, 2 & 6). The density of these sexine elements is very variable even within the same sample. If fairly densely arranged the unevenly outlined or interrupted 'islands' of sexine at the poles may be considered, but doubtfully, rudimentary apocolpia. The situation appears to be close to what Barth & Barbosa (1972) would call irregularly parasyncolpate (p.469: 'irregularmente parassincolpado'). Sexine sculpture of the mesocolpia is reasonably constant within a sample but the coarseness of the pattern usually varies between samples.

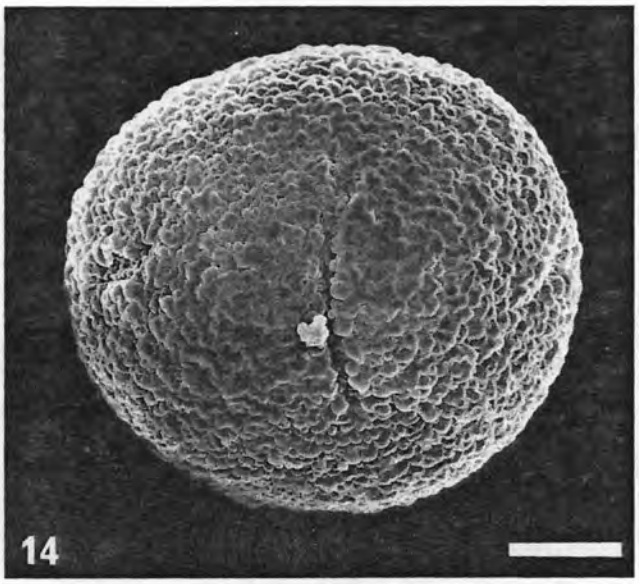
Pollen type B (hermaphrodite flowers)

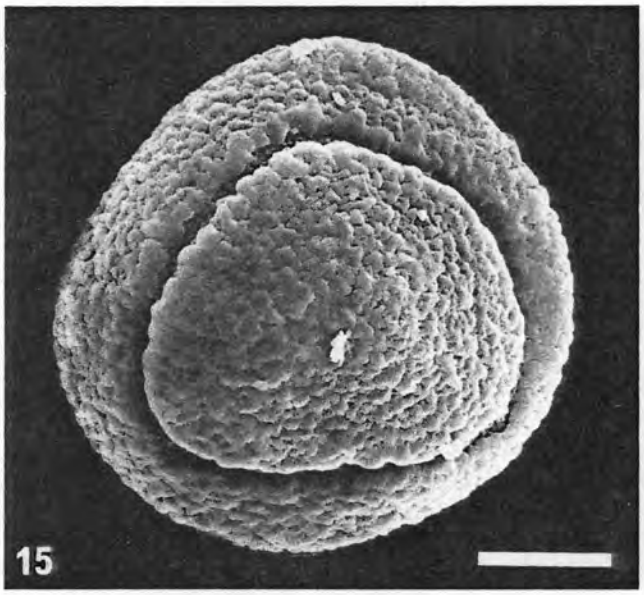
Pollen shed as monads. Grains radially symmetrical, apolar or heteropolar, spheroidal, (22)28 – 35(40) µm equatorial diameter. Outline circular. Grains atreme [inaperturate] or colpate (colpi often not discernible with the LM). Colpus or colpi (if present) well defined, *ca.* 0,5 µm wide and of variable length, usually continuous, forming variable but occasionally more or less circular patterns often confined to one hemisphere (grains then considered heteropolar). Ora and vestibula absent. Exine 2 – 2,5 µm thick, sexine and nexine not clearly distinguishable. Sexine sculpture as in pollen type A. Colpus membrane more or less granulate.

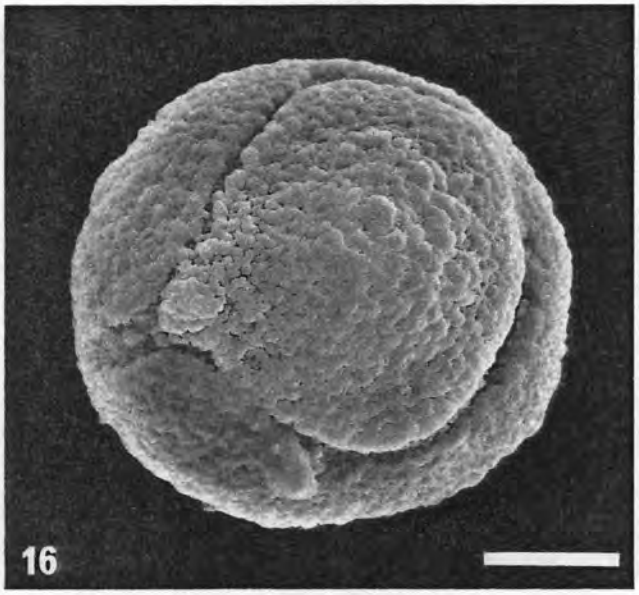


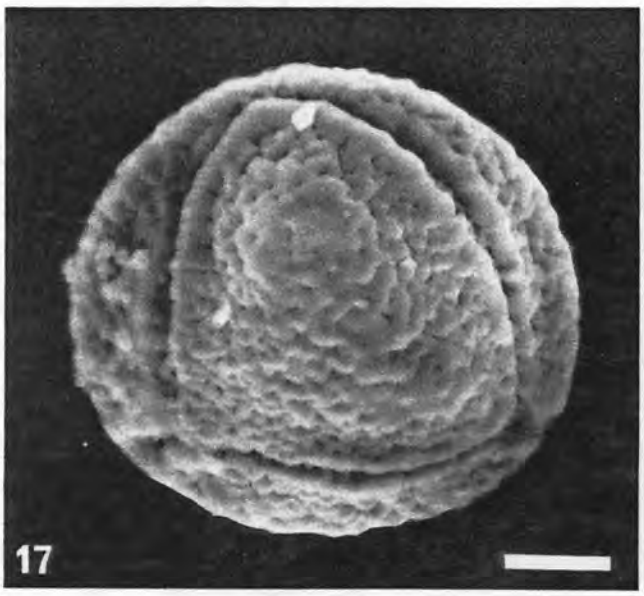
Figures 7 – 12 Pollen from male plants. LM micrographs of grains in polar view. **7 & 8.** *E. natalitia* (*Van Wyk 5988*), surface focus and optical cross-section, respectively (different grains). **9.** *E. woodii* (*Van Wyk 5578*), compare Figure 4. **10.** *E. simii* (*Van Wyk 4176*) showing very narrow vestibula in optical cross-section — compare Figure 12. **11 & 12.** *E. simii* (*Van Wyk 4178*), surface focus and optical cross-section, respectively (same grain) — note conspicuous vestibula in 12. Scale line = 10 µm.

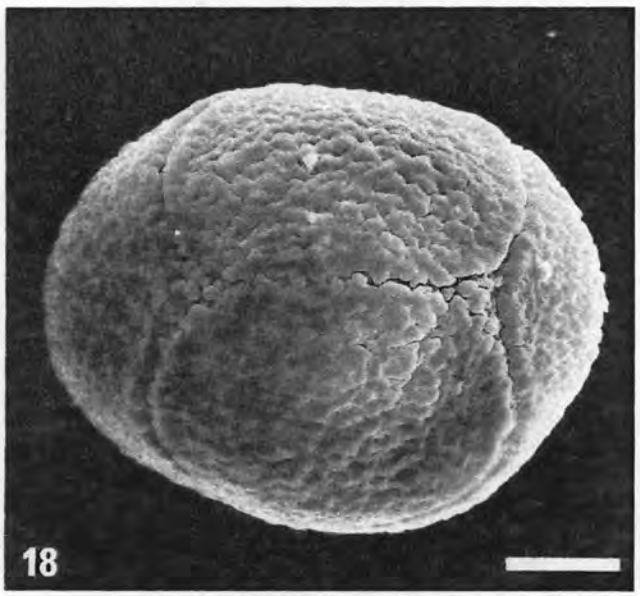










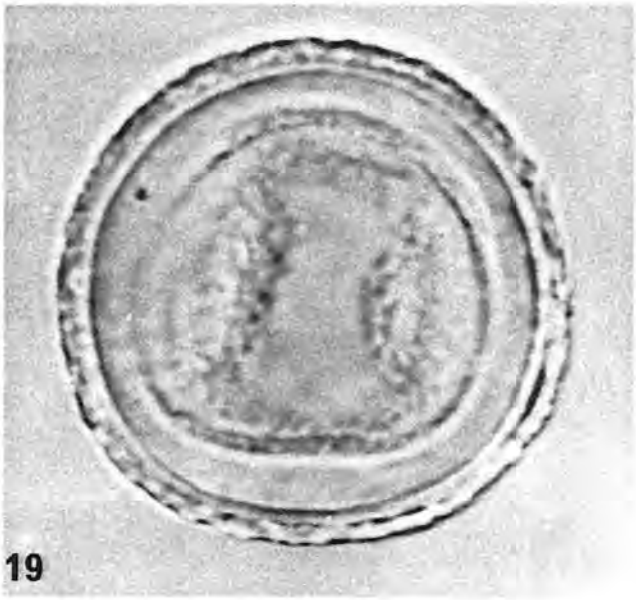


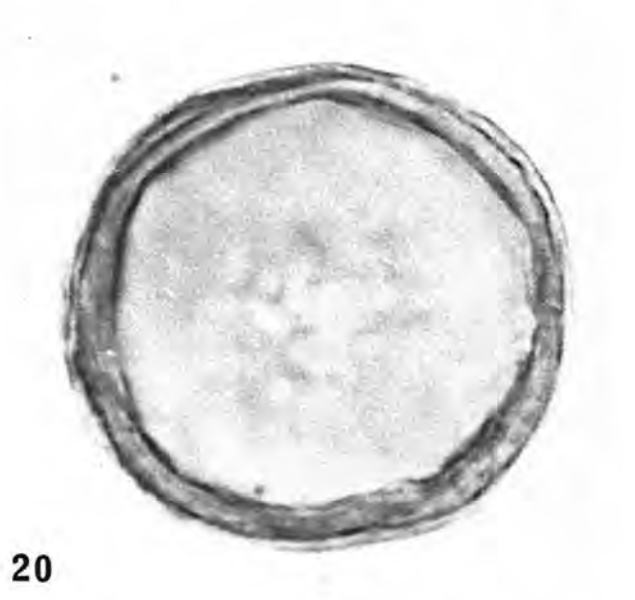
Figures 13 – 18 Pollen from hermaphrodite plants. SEM micrographs showing variable pattern of colpi. **13.** *E. simii* (*Van Wyk 4175*), atreme although colpus could be present on other side. **14.** *E.* cf. *mossambicensis* (*Van Wyk 2494*) showing a short colpoid streak. **15 & 16.** *E. woodii* (*Muller 3736*) showing ± circular colpoid streaks. **17.** *E. zuluensis* (*Van Wyk 3294*). **18.** *E. albanensis* (*Abbott 335*). Scale line = 5 µm.

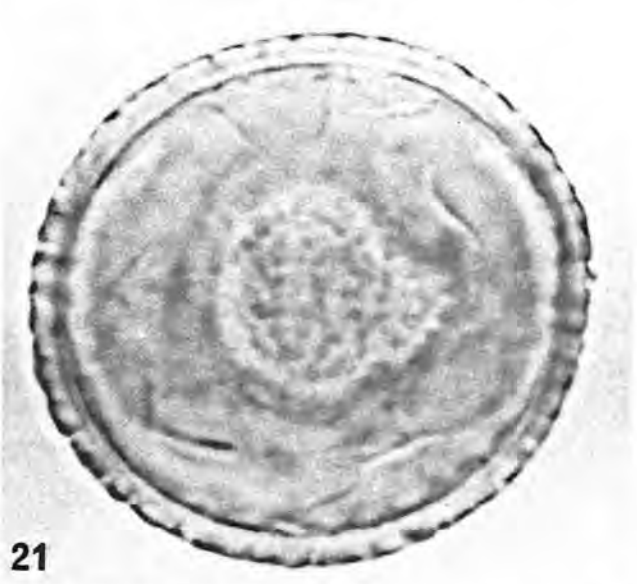
Pollen type B also shows intraspecific variation in characters such as grain size, coarseness of sexine sculpture and particularly the occurrence and pattern of the colpus (or colpi). Grains up to 40 µm in diameter were recorded in some samples of *E. capensis* and *E. simii*. Although this relatively large grain size is not constant for the species, the potential to produce grains this size could perhaps well be. However, many more samples need to be studied to substantiate such a claim. In the majority of investigated samples grain size ranged from 28 – 35 µm. Both apparently atreme and colpate grains were present in each sample — the relative proportions varying from sample to sample. Many different, usually asymmetrical, colpus patterns were present in a sample (Figures 13 – 19). A single colpus forming a more or less circular pattern of variable size was encountered quite frequently (Figures 15 & 16). However, the typical myrtaceous tricolporate pattern recorded in pollen type A was never recorded in pollen type B. Although sexine sculpture resembles that of pollen type A, a tendency for the supratectal processes to coalesce, resulting in scattered smooth surfaced areas, was observed in some samples of *E. simii* and *E. capensis* (Figure 13).

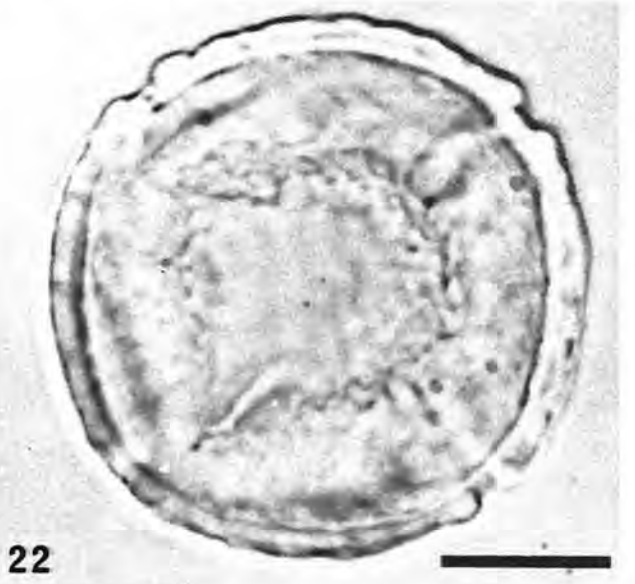
Discussion

In general the pollen grains of Myrtaceae are free, small to medium, radially symmetrical, isopolar, tricolporate, goniotreme, oblate-elliptical, syncolpate or parasyncolpate with a triangular amb and a smooth or faintly patterned sexine surface (Erdtman 1952, 1966; Pike 1956; McIntyre 1963; Gadek & Martin 1981; Patel *et al.* 1984). Pollen type A is therefore typically myrtaceous. It is morphologically similar to the pollen of *Eugenia s.str.* species from both the New World (Fernandes 1967; Barth & Barbosa 1972; Lieu & Melhem 1973; Carreira 1976; Graham 1980) and other parts of the Old World (Kubitzki 1965). The observed intraspecific variation in pollen morphological features and the difficulty to apply these features taxonomically at the species level also agree with the observations on *Eugenia* in other parts of the world (Barth









Figures 19 – 22 Pollen from hermaphrodite plants. LM micrographs of grains in optical cross-section. **19.** *E. woodii* (*Müller 3736*), compare Figures 15 & 16. **20.** *E. natalitia* (*Ward 5244*). **21 & 22.** *E. albanensis* (*Abbott 335*), different grains — note three colpoid grooves cutting through the sexine (?) in 22. Scale line = 10 µm.

& Barbosa 1972; Graham 1980).

Morphologically typical *Eugenia* pollen (*cf.* pollen type A in southern African species) cannot be distinguished from the pollen of a number of related as well as unrelated genera of the Myrtaceae (Pike 1956; Barth & Barbosa 1972; Lieu & Melhem 1973; Graham 1980). The diagnostic characters to differentiate between *Eugenia* and related genera claimed by Stellfeld (1968) do not seem to be valid in view of the few samples considered in the study. Hence, the lack of distinguishing features to differentiate between pollen type A in species groups X and Y does not necessarily either invalidate or justify the proposed taxonomic treatment of the southern African species of *Eugenia*.

This is the first report of dimorphic pollen occurring in Myrtaceae. The phenomenon went undetected when Pike (1956) studied two southern African species because both available samples were from male plants. Known cases of pollen dimorphism in other families are often associated with heterostyly (e.g. Erdtman 1952, 1969; Lewis 1979; Shivanna *et al.* 1983) and, with few exceptions (Baker 1956), lack the pronounced morphological differences encountered during the present study. It is also intriguing that the same phenomenon should be present in both species groups X and Y (which in many non-palynological features do not seem to be very closely related) but apparently absent in *Eugenia* from other parts of the world. Whether this represents parallel or convergent trends in specialization of the grains is not yet clear.

Pollen dimorphism also associated with morphological androdioecy and therefore rather similar to that in *Eugenia* was reported in species of *Tetracera* L. and *Saurauia* Willd. (Dilleniaceae) (Kubitzki & Baretta-Kuipers 1969; Haber & Bawa 1984). *Tetracera* is represented in both the New and Old Worlds but androdioecy is present only in the New World species. This is exactly the reverse of the situation in *Eugenia*. Male plants of *Tetracera* have tricolporate pollen (pollen type A) whereas that of hermaphrodites (although described as inaperturate) only has 5–7 endopores bordered by costae (pollen type B). The latter grains were assumed to be sterile and the authors suggested that the species involved were most probably functionally dioecious. In *Tetracera* pollen type A is confined to the Old World species (all with flowers hermaphrodite) and to male flowers of the New World species. Pollen type B only occurs in the hermaphrodite flowers of the New World species.

It is suspected that in *Eugenia* pollen type B is inviable (or almost so). This would mean that the southern African (and probably African) species of *Eugenia* are functionally dioecious and not truly androdioecious. This would tie in with the recent statement of Charlesworth (1984) that true androdioecy appears to be extremely rare. In fact, all the claimed cases of androdioecy reviewed by this author appear to involve functional dioecy, with females retaining substantial anther vestiges. Studies on the pollen viability and reproductive biology of *Eugenia* in southern Africa are under way and will be reported elsewhere.

Besides the presence of a sexine and nexine layer, LM analysis did not reveal structural elements in the exine of any of the investigated species of *Eugenia*. It should, however, be pointed out that in Myrtaceae the small grain size and the resolution of the LM limit the extent to which exine structure can be interpreted. Ultrastructural exine analysis by transmission electron microscopy of the grains of a number of species of Myrtaceae (not *Eugenia*) shows the presence of a somewhat unstructured, granulate infratectal layer and a granular/alveolate nexine layer around the ora (Lugardon & Van Campo 1978; Gadek & Martin 1982). Such a granulate infratectal layer is of restricted occurrence among angiosperm pollen (Van Campo 1976; Walker 1976).

We have no ontogenetic evidence for pollen of *Eugenia* to account for the morphological differences between pollen types A and B. However, Wodehouse (1935) concluded that the number and arrangement of apertures in the grains of most dicotyledons are determined by the tetrahedral or other arrangement incident to their formation in the tetrad. Consequently we postulate that in pollen type A the number and position of the colpi and ora are determined by the tetrahedral arrangement of the grains in the tetrad group. For pollen type B we postulate that either the four daughter cells produced by meiosis do not get into the tetrahedral position but assume some other arrangement, or that the pollen mother cells do not undergo meiosis but develop directly into pollen grains (perhaps preceded by some mitotic divisions). Presumably the latter grains are produced only to attract pollinators and it is therefore quite possible that meiosis could have become redundant. The tendency for the colpi to coalesce and to form asymmetrical patterns in these spheroidal grains also seems to conform to predictions based on the 'Law of equal triconvergent angles' proposed by Wodehouse (1935).

It would be of interest to learn whether evidence from fossil pollen grains could shed some light on the evolutionary sequence that produced the existing sexual state in African species of *Eugenia*. The distribution pattern of Myrtaceae is clearly Gondwanic (Johnson & Briggs 1981) and microfossils attributed to Myrtaceae are common in geological deposits of various ages, especially those of the Cenozoic (e.g. Pike 1956; McIntyre 1963; Graham 1980; Coetzee *et al.* 1983). We would therefore like to alert students of geopalynology to be on the look-out for grains similar to type B. These grains are very distinctive but so different from typical Myrtaceae pollen that, if they have been encountered in the past, they have probably never been linked to this family.

Acknowledgements

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CHAPTER 9

STUDIES ON THE REPRODUCTIVE BIOLOGY*

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STUDIES ON THE REPRODUCTIVE BIOLOGY OF EUGENIA L. (MYRTACEAE) IN SOUTHERN AFRICA

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&

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Eugenia in southern Africa displays morphological androdioecy. Pollen grains are tricolporate in males and colpate or inaperturate in hermaphrodites thereby suggesting that the species could be functionally dioecious. The present report includes a general assessment of pollen viability in a number of species, and an in-depth study of the reproductive biology in E. simii. Pollen grains from males were found to germinate readily whereas those from hermaphrodites were practically inviable. Both types of pollen usually contain a small percentage of aborted grains. Native species of Eugenia are therefore functionally dioecious, thereby supporting the recent claim that in all known cases of morphological androdioecy, functional androdioecy probably does not occur. Neither of the floral types produce nectar but the anthers and pollen grains emit a strong sweet odour. The retainment of pollen producing anthers in females probably serves as a lure to attract pollinators. Honey bees were seen to visit the flowers but other insect species probably also act as pollen vectors. A statistically significant male-biased sex ratio was found in the largest known population of E. simii. Casual observations also suggest male-predominant sex ratios in many populations of the other species. No species is gynodioecious and no evidence of apomixis was found. Preliminary bagging experiments show that fruit is only produced by bisexual flowers pollinated with grains from male flowers. Sexual dimorphism is rare in Myrtaceae and has not yet been recorded in Eugenia outside Africa. Dioecy in the African species of Eugenia may have evolved directly from hermaphroditism, or via androdioecy or gynodioecy. Curiously, this functional dioecy is present in two groups of species which on other grounds do not seem to be closely related.

1. INTRODUCTION

Eugenia is a large pantropical genus with several hundred species concentrated in Central and South America. It is poorly represented in Africa and the rest of the Old World. The small group of African species is of considerable interest in being the only known members of the genus which display sexual dimorphism - a phenomenon relatively rare in the Myrtaceae.

About 15 species of *Eugenia* are native to southern Africa. These fall into two major supraspecific groups (provisionally referred to as species groups X and Y) delimited by various morphological and anatomical characters (Van Wyk 1978, 1980a, 1985b; Van Wyk *et al.* 1980, 1982; Van Wyk & Botha 1984). Natural populations of all the native species are androdioecious, consisting of plants with either morphologically male or morphologically hermaphrodite flowers. Androdioecy is considered very rare among flowering plants (Lloyd 1975; Charlesworth & Charlesworth 1978; Bawa 1980; Willson 1983).

In a recent review of the phenomenon of androdioecy in seed plants, Charlesworth (1984) argues that, while plant populations do exhibit morphological androdioecy, in all known cases functional androdioecy probably does not occur. These morphologically androdioecious plants are in fact functionally dioecious. Several features of the taxa indicate functional dioecy (Charlesworth 1984). These features include 1:1 sex ratios, inaperturate and/or non-germinable pollen in bisexual flowers, and indehiscent anthers. In addition, all probably lack nectar indicating pollination either by wind or pollen-gathering bees.

The evolution of dioecy has attracted much attention in recent years (e.g. Bawa 1980, 1984; Ross 1982). If functional androdioecy is of extremely rare occurrence if at all, then the claims that androdioecy may be an important pathway in the evolution of dioecy (Bawa & Beach 1981; Ross 1982) are not valid.

An assessment of the taxonomic significance of pollen morpho= logy in 14 southern African species of Eugenia, showed that all the investigated species produce pronounced dimorphic pollen (Van Wyk & Dedekind 1985). Pollen grains are tricolporate in males and colpate or inaperturate in hermaphrodites. The lack of ora (endopores) suggests that the grains from hermaphrodites may be inviable (or nearly so), thus rendering the flowers functionally female. This prompted the present study which includes a general assessment of pollen viability in a number of species, and a more detailed study into the biology of sex expression in E. simii Duemmer. The major objective was to determine whether Eugenia in southern Africa is functionally androdioecious, or as predicted by Charlesworth (1984) and suggested by pollen morphology, functionally dioecious.

Available information on breeding systems in Eugenia (and the Myrtoideae in general) is meagre. It is suggested that a compara= tive study of breeding systems in Eugenia may provide an understand= ing of the possible evolution of dioecism via androdioecy in particu= lar. Therefore the present paper also attempts to bring together some evidence and speculations on the reproductive biology of Eugenia in southern Africa derived from the scattered literature, and casual observations made over several years of field work. Although incom= plete, it is presented with the hope that it may encourage more de= tailed observations and serve as the basis for intensive future in= vestigation.

2. MATERIALS AND METHODS

2.1 Pollen viability

A list of southern African species of Eugenia arranged according to their supraspecific group is supplied in Table 1. Pollen viability was determined for both sex forms in E. capensis, E. natalitia, E. simii,

E. woodii and E. zeyheri, all which were available from botanical and private gardens in Pretoria. Voucher specimens are housed in the H.G.W.J.Schweickerdt Herbarium (PRU).

The hanging drop technique (Stanley & Linskens 1974) has been adopted for the in vitro pollen germination testing. Distilled water containing 0,01% boric acid and varying sucrose concentrations was used as the basic germination medium. All samples (from one male and one female plant per species) were tested at concentrations of 5, 10, 15, 20 and 30% sucrose. As calcium was found to promote the growth of pollen tubes in certain groups (Shivanna et al. 1983), all tests were repeated with calcium added to the basic medium at a concentration of 2×10^{-3} mol. dm^{-3} $Ca(NO_3)_2$.

Pollen was collected shortly after sunrise from newly opened flowers. Samples were taken directly from a dehiscing anther and dusted onto the drop of medium. These were then incubated at 27°C. Observations of germination percentage and tube length were made at regular intervals spread over 3 days.

Alexander's viability stain (Alexander 1969) was used for the differential staining of aborted and non-aborted pollen grains. Stainability was assessed in freshly collected pollen samples from the same plants in which pollen germination was tested.

For the examination of pollen tubes in the style, open-pollinated flowers of E. simii in which fruit development had just commenced were fixed in FAA. The styles (which persist for some time after flowering) were cleared and softened in 0,8 mol·dm^{-3} NaOH at 60°C for 1 hour, stained with 0,1% water soluble aniline blue in 0,1 N $K_3PO_4 \cdot 7 H_2O$ for at least 10 minutes, squashed in a drop of staining medium and viewed under ultraviolet light (Martin 1959).

2.2 Pollen reserves

For detecting the presence of starch, mature pollen grains from

freshly dehisced anthers were squashed in potassium iodide-iodine (IKI)(Johansen 1940) and examined under the light microscope (Baker & Baker 1979). The presence of oil droplets (confirmed by staining with Sudan Black B) was also recorded.

2.3 Odour production

To locate the source of odour production different floral parts were cut off and kept for some time in closed vials. Vials containing anthers with pollen, filaments, petals and the remaining receptacle with ovary and calyx lobes were prepared. Accumulated odoriferous substances are easily smelled when a vial is opened. For the location of osmophores fresh flowers were dipped for ± 5 hours in a 0,1% solution of neutral-red in water (Vogel 1962). Care was taken not to bruise floral parts during handling.

2.4 Field observations

Field observations and bagging experiments were conducted during October 1984 on *E. simii*, a riverine shrub endemic to southern Natal. This species was selected because of its gregarious habit, fairly regular flowering and easily accessible flowers. Sex ratios were determined in three populations : one on an island in the Umtamvuna River near Port Edward (UR), a second relatively small population along the Uvongo River near Uvongo (UVR) and thirdly the largest known population near the bridge over the Umzimkulwana River in the Oribi Gorge Nature Reserve (OG). In each population over 50% of the individuals were flowering and thus could be sexed. No instances of sexual variation within a plant were observed.

Determination of natural fruit set and bagging experiments to test for self-fertilization and non-pseudogamous apomixis were carried out on plants in the UR population only, because of the relative inaccessibility of the other two populations for long term experiments.

Six individuals (three males and three hermaphrodites) were studied in the UR population. To assess natural fruit set branches with flowers past anthesis (on males) or with withered styles (on hermaphrodites) were bagged with nylon stocking. Branches having unopened flowers were bagged to test for self-fertilization. Un= opened flowers also were emasculated and bagged to test for fruit set indicating non-pseudogamous apomixis. All branches with the various treatments were collected two months later and any maturing fruits and/or abscised flowers were counted.

3. RESULTS

The suspicion that the southern African species of Eugenia are functionally dioecious is supported by the information presented in this paper. We shall subsequently consider the plants with mor= phologically hermaphrodite flowers as females and refer to their flowers as female flowers.

3.1 Flowering time, inflorescence structure and floral morphology

Although odd flowering specimens may be found throughout the year, all the native species of Eugenia clearly display a peak flowering season. E. capensis and E. cf. mossambicensis flower in early summer, E. verdoorniae in winter and the remainder of the species in spring. Individuals and even whole populations may skip flowering for one or more seasons. This is particularly the case in species belonging to group Y (Table 1). Drought conditions seem to be a major factor responsible for delayed flowering. New growth and flowering in the rhizomatous geoxylic suffrutex, E. albanensis, are promoted by grassland fires (Van Wyk 1985). This is probably also the case in E. cf. mossambicensis and E. pusilla which have a similar habit. Most plants in an area are approximately synchronous in flowering.

Depending on the species, flowers are borne solitary, in fas=cicles, small racemes or cymules. These are positioned predominant=ly laterally on the shoots. In species group Y flowers are carried mainly at the first few nodes of the new season's growth. In species group X the flowers tend to predominate on the previous season's growth and some specimens may be distinctly ramiflorous. Inflorescence structure will be discussed in more detail in a forthcoming paper.

One gains the impression that male plants tend to be more flori=ferous than females. However, detailed field observations on E. simii have shown that some females can be just as floriferous as males. Only plants in flower or fruit can be sexed.

The basic floral construction is similar in all the native species of Eugenia. Drawings and detailed descriptions of male and female flowers are provided in Van Wyk (1979, 1980b & 1982). Flowers of E. simii are illustrated in Figures 1 & 2.

Female flowers are actinomorphic with four calyx lobes, four free petals, 10 to numerous free stamens borne on a flat 'disc' sur=rounding the base of the style, an inferior usually bilocular ovary and a style with a simple or bifid(E. capensis and E. cf. mossambicen=sis) stigma. Stigmas are of the 'dry' type, as in other Myrtaceae (Heslop-Harrison & Shivanna 1977). Nectaries are absent. Viewed from above, all floral parts are usually more or less white. Petals are occasionally pinkish coloured in individuals of some species. Calyx lobes and the hypanthium (floral tube) - the latter which is not prolonged beyond the summit of the ovary - are green. The stamens are perfectly normal and the flowers appear hermaphroditic.

In male flowers the ovary is rudimentary or sometimes apparently absent. A short (ca. 1mm long) stylar protuberance and rudimentary ovules are occasionally present. The hypanthium forms a hollow cup and appears less 'swollen' from the outside than in female flowers.

Otherwise male floral parts are similar to those of female flowers.

Anthers are similar in male and female flowers and abundant pollen is shed after the thecae have dehisced longitudinally. Each anther connective has a terminal secretory cavity - a feature typical of the Myrtaceae.

In any one population the stamens in female flowers tend to be slightly fewer and shorter than their male counterparts. For example, in E. woodii male flowers have 20-30 and female flowers 10-20 stamens (Van Wyk 1980b). In E. verdoorniae stamen number varies from (14) 16-20 (22) in males and (11) 14-16 (20) in females (Van Wyk 1979). In E. erythrophylla the filaments are 4-5 mm long in male flowers and 3-5 mm long in female flowers (Strey 1972). The latter author also pointed out that the petals in female flowers are somewhat larger than in males. In all the native species of Eugenia the two flower types (for a species) have approximately the same diameter.

3.2 Nectar and odour production

Male and female flowers do not produce nectar but the anthers and pollen grains emit a strong sweet odour. The intensity of the odour varies between samples and this deserves further study. No significant odour was detected in other floral parts.

Staining with neutral-red did not reveal any osmophores. Anthers (only if dehisced) and pollen grains stain red but this can be explain= ed by the fact that the stain is effective in areas lacking an intact cuticular membrane. The correlation between the source of the odour and the areas stained is accidental.

We were unable to demonstrate whether the original source of the odour is the tissues of the anther or the pollen grains (or perhaps both).

3.3 Pollen morphology

The anthers within a single flower dehisce more or less simul= taneously to release the creamish coloured pollen grains. Grains

are slightly 'sticky' and clump together. Detailed descriptions of the morphology of the dimorphic pollen grains are supplied in Van Wyk & Dedekind (1985). Only the outstanding diagnostic charac= ters are summarized below. It was impossible to differentiate be= tween species on the basis of palynological features.

Pollen of male flowers is typically myrtaceous and resembles that of hermaphroditic species of Eugenia in other parts of the World. Grains are free, radially symmetrical, isopolar, oblate to peroblate, (17) 20-25 (30) µm equatorial diameter, triangular, goniotreme and tricolporate (Figure 4).

Pollen from female flowers deviates considerably from the typical myrtaceous pattern. Grains are free, radially symmetrical, apolar or heteropolar, spheroidal, (22) 28-35 (40) µm diameter and atreme or colpate (Figure 3).

In nearly all the samples studied only one type of pollen morph was present in a particular flower. However, in one or two samples of female flowers a few apparently normal male-type grains were noticed. Occasional female-type grains were also spotted in a few pollen samples from male flowers. It is likely that at least some of the foreign grains were brought in by pollen vectors (flowers were unbagged). The possibility that male flowers occasionally produce a few female-type pollen grains, and vice versa, nevertheless exists and deserves further investigation.

The staining tests for lipids and starch grains were positive only for lipids. No starch grains were detected. The lipids were in the form of small oil globules.

3.4 Pollen viability

The use of Alexander's stain showed that all pollen samples con= tain some aborted grains (Figures 3 & 4). The amount of aborted grains may vary from anther to anther but was nearly always less than

20% and in many samples not more than 5%.

Germination results with male pollen (Figure 6) were rather inconsistent. The germination percentage varied between samples from different anthers in the same flower and between different flowers from the same plant. Whereas pollen from one flower would give an almost 90% germination, samples from a neighbouring one would fail to germinate. However, such extremes were the exception. Male pollen germinated in a range of sucrose concentrations from 5-30% with perhaps an optimum between 5 and 20%. Pollen from one sample of E. woodii even germinated in distilled water! The introduction of calcium in the medium did not give an improved germination or significantly longer tubes. In fact, germination percentages tended to be slightly higher on the basic medium. For most samples germination percentages between 50 and 80% were obtained. The first germinations usually occur within 1-2 hours of commencement of the test and the percentage germination increases rapidly with increasing time. The maximum germination percentage is normally reached within 24 hours. No pollen tube bursting was observed, even at low sucrose concentrations.

Pollen from female flowers is considered inviable. Only three out of thousands of observed grains showed signs of germination (Figure 5). These were observed in a single sample of E. natalitia. However, the pollen was obtained from an unbagged flower and the possibility of contamination exists. If it was in fact Eugenia grains, the relatively short tubes (compared with length of pollen tubes in males) suggest that they may be unable to reach the ovules.

Cleared styles and stigmas of E. simii showed that although abundant female grains are present on the stigma, these do not germinate (Figure 8). Also present were numerous male grains, the majority which were found to have germinated. The very large number

of fluorescent pollen tubes penetrating the style on their way to the ovules indicate that there must be intense competition among the male pollen grains on a stigma (Figure 7).

3.5 Pollen vectors

There is still some doubt as to the principal pollinators of Eugenia in southern Africa. While inspecting populations of E.simii, very few potential pollen vectors was noticed. However, the cool, cloudy weather prevailing at the time could have slowed down insect activity. The only fairly frequent visitors observed on flowering specimens of Eugenia growing in Pretoria were honey bees. Honey bees were also seen to be active in natural populations of E.capensis. The native species of Eugenia provisionally are considered to be bee-pollinated.

3.6 Fruit set and seed dispersal

Table 2 details the percentage fruit set on plants of E. simii under natural conditions. Only bisexual plants produce fruits. It is clear that the plants vary considerably in the percentage of fruits set, from 22 to 66% of the flowers maturing to fruits. Further studies are needed to determine the possible causes of such variation including those of pollinator activity, proximity to male plants, and microhabitat differences.

Cultivated plants of other Eugenia species also only produce fruits if they are bisexual. Despite abundant flowering, single female individuals of E. capensis, E. natalitia and E. zeyheri culti=vated in isolation from male plants of the species did not set fruit. Curiously, a few fruits were spotted on two adjacent female plants of E. woodii on the campus of the University of Pretoria. The nearest known male plant is in a garden several kilometers away. Considering the very large number of flowers produced by these females, the five

fruits may seem negligible. However, it gives rise to a number of questions which require further study.

Fruits of Eugenia in southern Africa are fleshy berries which are nearly always one (rarely up to three) seeded. Ripening is usually slightly asynchronous and accompanied by a sequential colour change. Seed structure is described by Van Wyk (1980a). Van Wyk & Botha (1984) presents information on seed ontogeny.

Fruits of species group X usually ripen in a colour sequence from green through yellow or reddish-orange to dark purple or blueish-purple, sometimes even appearing almost black. The pulp of the fruit is whitish in colour and not very tasty. Abundant secretory cavities dot the surface of the fleshy embryo which is contained in a relatively thin testa.

Fruits of species group Y usually ripen in a colour sequence from green through yellow and reddish orange, eventually becoming bright red. The pulp of the fruit is yellowish and tasty. The fleshy embryo is virtually eglandular and contained in a relatively thick woody testa.

There is a need for more field observations on the mode of seed dispersal. It is possible that birds may be the principal agents of dispersal. In forest species, ripe fruits are rapidly removed by vervet and samango monkeys (the latter are particularly fond of E. zuluensis), baboons and red squirrels. Within species group Y, E. albanensis is the species with the smallest habit (a grassland suf= frutex whereas other members are forest trees), but it produces the largest fruits (up to 50 mm diam.). When ripe these fruits are often concealed by a dense cover of grass (Van Wyk 1985). How the relatively large seeds are dispersed, is still unknown.

3.7 Sex ratios

Results of the sex ratio determination in the three populations of E. simii are presented in Table 3. Although the two small populations

have a 1 : 1 sex ratio, the largest population in Oribi Gorge has a statistically significant male-biased sex ratio. This is somewhat unexpected given that previous studies of putatively androdioecious genera have shown a 1 : 1 ratio indicating functional dioecy (Charlesworth 1984).

Casual observations made by the senior author over several years at various sites indicate that males seemingly tend to outnumber females. This phenomenon has made it difficult to obtain adequate female flowering material in some species (female flowers display more taxonomically useful features). A paucity of female flowering specimens (at least in some species) also prevails in herbaria. All the fertile specimens of six species of Eugenia in the National Herbarium (PRE) are sorted according to sex in Table 4 (specimens collected by the senior author were not taken into account because they are female biased). However, other factors besides a naturally skewed sex ratio may also account for these herbarium statistics (see Discussion).

3.8 Tests for selfing and non-pseudogamous apomixis on E. simii

A total of 66 bisexual flowers and 48 male flowers were bagged to test for the presence of self-fertilization. All flowers abscised without producing fruits. Eleven bisexual flowers and 10 male flowers that were emasculated and bagged also abscised without producing fruit. These results indicate the lack of self-fertilization and although the sample size is small also indicate that non-pseudogamous apomixis is not operative. In the field no male plants of any southern African Eugenia species have been observed by either author to produce fruits.

4. DISCUSSION

4.1 Sexual dimorphism in Eugenia and some other Myrtoideae

Sexual dimorphism in African species of Eugenia has generally been overlooked in older works (e.g. Niedenzu 1893). Lawson (1871) referred to a specimen of E. calophylloides with staminate flowers but did not elaborate on the phenomenon. Engler & Von Brehmer (1917) and Engler (1921) distinguished two groups of Eugenia species in Africa : a group with the gynoecium sunken into the receptacle and a group with the gynoecium not sunken into the receptacle. Obviously these groups were based on specimens with male and female flowers, respectively. The suspicion was nevertheless voiced that the group with sunken gynoecia may repre= sent a stage in the reduction of hermaphrodite flowers to unisexual (male) ones (Engler & Von Brehmer 1917 p.334).

Amshoff (1958) noted that the African species of Eugenia are "as a rule polygamous or (in E. tisserantii Aubréville et Pellegrin accord= ing to the collector) dioecious". That flowers of at least some southern African species of Eugenia are polygamous, was evidently known by authors such as Thonner (1908), Duemmer (1912) and Marloth (1925). More recently, White (1978) noted that all the species of Eugenia in the Flora Zambesiaca area display sexual dimorphism.

Amshoff (1958) claimed that if the flowers are polygamous, there may be several male flowers and one or two hermaphroditic flowers in the same fascicle. White (1978) also maintained that hermaphroditic flowers are sometimes accompanied by apparently functionally male flowers. Evidence from the present study casts some doubt on these claims, which we unfortunately were unable to verify. During more than ten years of work on Eugenia in southern Africa, the senior author has only once found a male flower among spirit material supposed to be female (then still regarded as hermaphroditic). This led to the description of E. verdoorniae as "... androdioecious or andromonoecious ..." (Van Wyk 1979). Subsequent efforts to find male flowers on females failed and

it is now thought that the original observation could have been based on an accidentally mixed collection. Neither was any evidence found for the presence of female (or morphologically hermaphrodite) flowers in males (gynodioecy). According to Wood (1902) the short-styled flowers in E. albanensis represent a developmental stage which is subsequently followed by a lengthening of the style. This was not confirmed by the observations of White (1978). Our observations also refuted the claim by Wood, which is undoubtedly wrong.

All the southern African species of Eugenia are morphologically androdioecious, and there is reason to suspect that this is the prevailing state in most (if not all) African members of the genus. This study has also shown that the species investigated to date are functionally dioecious. This ties in with the recent statement of Charlesworth (1984) that true androdioecy appears to be extremely rare. In fact, all the claimed cases of androdioecy reviewed by the latter author appear to involve functional dioecy (with the possible exception of Xerospermum intermedium, cf. Appanah 1982), with females retaining substantial anther vestiges. In Myrtaceae, androdioecy has been reported in Decaspermum (Niedenzu 1893; Yampolsky & Yampolsky 1922), but this needs confirmation as no detailed data are available. Lack & Kevan (1984) recorded that pollen of D. parviflorum was collected by large numbers of insects.

Significantly, no New World species of Eugenia, nor Old World non-African species of Eugenia have been reported to have sexual dimorphism in their flowers. Dioecy is relatively rare in Myrtaceae and the family is for example not listed in a recent compilation of the occurrence of dioecy at the familial level (Givnish 1982). However,

dioecy can easily be overlooked. Elsewhere in the Myrtoideae Pimento dioica (allspice) has a hermaphroditic floral structure but functions as a dioecious species (Chapman & Glasgow 1961; Chapman 1964). In this species male and female flowers appear rather similar and even the pollen grains from both floral types are morphologically alike. Germination tests have, however, shown that 'female' pollen is practically inviable (Chapman 1964).

4.2 Floral and functional dioecy

The sexual system in the native species of Eugenia recalls that in dioecious species of Solanum (Anderson 1979; Symon 1979; Haber & Bawa 1984), some species of Tetracera and in particular Saurauia veraguensis of the Dilleniaceae (Kubitzki & Baretta-Kuipers 1969; Haber & Bawa 1984), Thalictrum polygamum of the Ranunculaceae (Kaplan & Mulcahy 1971; Melampy & Hayworth 1980) and Actinidia chinensis of the Actinidiaceae (Schmid 1978). In flowers of these taxa little, if any, nectar is secreted and the female flowers produce inviable (often inaperturate) pollen. The latter type of pollen obviously serves as a pollinator attractant and/or reward comparable with the phenomenon of feeding anthers in the flowers of some groups (Van der Pijl 1978; Faegri & Van der Pijl 1979).

On the basis of their numerous stamens and production of great quantities of pollen the flowers of Eugenia may be classified as typical pollen flowers of the so-called Papaver-type (cf. Vogel 1978 and Faegri & Van der Pijl 1979). This particular type of pollen flower also occurs in the Ranunculaceae, Actinidiaceae and Dilleniaceae (Vogel 1978). It has been noted above that a state of functional dioecy comparable to

that in Eugenia also prevails in some members of these families. This may demonstrate that the coevolution with pollen-utilizing insects such as Apidae may lead to a similar form of dioecism in non-related groups. The retainment of pollen production in female flowers allegedly overcomes the expected impediment which the lack of pollinator reward would have had on the evolution of dioecy in these groups (Baker 1984). Baker & Cox (1984) also pointed out that both male and female flowers must attract the same visitors, therefore a similar morphological appearance would be advantageous.

4.3 Floral morphology and pollinator foraging

Beach (1981) has discussed patterns of selective pollinator foraging as one of the possible causative agents in the evolution of dioecy. In this connection Bawa & Opler (1975), Bawa (1974, 1980) and Givnish (1982) have drawn attention to the frequent occurrence in dioecious tree species of small, relatively inconspicuous, white, yellowish or greenish flowers, pollinated by small bees or generalist insects. Bawa & Opler (1975) speculated that in obligately outcrossed species, pollination efficiency may be limited if a hermaphroditic flower's own pollen occupies some of the available space on the stigma. Under such conditions the development of dioecy may reduce the amount of pollen clogging on stigmas that occurs when small insects forage geitonogamously on large crowns. Judged by the large number of pollen tubes in the styles, the presence of many sterile pollen grains on the stigmas of female flowers in Eugenia does not seem to be a major impediment to pollination success.

The flowers of Myrtaceae are claimed to be predominantly zoophilous and nectariferous (Johnson & Briggs 1981). However, a study of Eugenia,

Cleistocalyx and Syzygium in Ceylon showed that nectarial tissue inside the staminal disc is rare (unfortunately no species were listed) (Kostermans 1981). An ovarian annular type of nectary is present in some species of Syzygium (Schmid 1972a) - see Lack & Kevan (1984) for details on nectar secretion in S. syzygioides. Schmid (1972b) did not report the presence of conspicuous nectaries in flowers of Eugenia s. str. We could also not trace any reports on the secretion of nectar in flowers of this genus, an aspect in need of more extensive field observation.

The odour produced by the Eugenia pollen grains and anthers may play a role in the recognition and detection of the flowers by pollinators. Particularly in the case of honey bees the odour of the pollen grains brought back to the hive may assist in the relocation of the flowers. The keen ability of honey bees to differentiate between odours was clearly demonstrated by Von Frisch (1923/24). Whether there may also be some pollinators acting as perfume-collectors (Vogel 1966) involved, needs to be determined.

Besides nectar, pollen is the most sought-after floral reward (Kevan & Baker 1983). The present study supports the statement by the latter authors that lipid-rich pollen grains are particularly common in species where pollen is the only floral reward offered. Baker & Baker (1979) reported that the Myrtaceae may be characterized by starchless mature pollen grains. They also showed that lipids are a major constituent of pollen grains in bee-pollinated flowers. However, a correlation also exists between the size of the grain and the nature of its reserve substances (Baker & Baker 1979). The fact that lipids are common in Myrtaceae may therefore also be due to the relatively small grains of the family.

4.4 Pollen germination and fruit dispersal

The variation in germination results obtained with male pollen grains may be due to a desiccation requirement. Elsewhere in the Myrtaceae, Boden (1958) has shown that a period of desiccation is needed to get optimal germination of pollen grains in Eucalyptus viminalis. It is possible that some of the Eugenia pollen samples tested were too fresh.

The colour sequence displayed by ripening Eugenia fruits strengthens the suspicion that birds may play an important role in the seed dispersal of most species. It has been shown in other groups that bicoloured fruiting displays (black and red) significantly enhance fruit removal by frugivorous birds (Mordan-Moore & Willson 1982; Willson 1983; Willson & Melampy 1983). Our findings on Eugenia support the observation that dioecy seems to be particularly prevalent among species with fleshy, bird-dispersed fruits (Bawa 1980; Givnish 1980, 1982). It also supports the observed association between dioecy and the production of single- or few-seeded fruits (Bawa 1980; Willson 1983).

The distinct differences in fruit and particularly seed morphology between species groups X and Y are in marked contrast to the fairly similar floral construction and sexual state of the flowers of all the species. This gives rise to several questions, the answers of which may be the subject of considerable speculation. For example: Could the present distinctions between groups X and Y perhaps reflect a difference in the particular seed predators or dispersal agents with which two initially closely related taxa have evolved? Could the two groups perhaps represent the end result of two distinct evolutionary lines derived from fairly distantly related ancestral stocks which were subsequently subjected to the same selective pressures (in other words,

has there been convergence)? Is the relatively thick testa in species group Y perhaps a measure to counteract the increase in potential dangers which the presence of a tasty pericarp may hold for the embryo? On the other hand, does the less tasty and more tanniniferous pericarp in species group X offer more protection to the embryo, thereby justifying the relatively thin testa? To answer these and other questions more field observations on the possible selective pressures imposed on the fruits and seeds are required.

4.5 Sex ratios

Selected data on sex ratios in adult dioecious (mainly morphologically) seed plants are summarized by Willson (1983). The preponderance of males is a common phenomenon. It may be caused by factors such as the differ= ential growth of pollen tubes, differential survival, environmentally determined lability of sex expression and other genetic and environmental factors (Lloyd 1974; Lloyd & Webb 1977; Opler & Bawa 1978; Willson 1983; Waser 1984). It would be interesting to see whether the germination of Eugenia seeds also yields a significantly male-biased sex ratio. Such a ratio may indicate the possible presence of differential fertilization.

A number of functionally dioecious (morphologically androdioecious) species reviewed by Charlesworth (1984) displayed 1:1 sex ratios. Appanah (1982) reported a similar sex ratio in Xerospermum intermedium (Sapindaceae), a structurally androdioecious but functionally dioecious species which may also be functionally androdioecious under certain experimental conditions. However, in this species male trees flower more frequently resulting in male-biased sex ratios if flowering specimens only are considered. Male-biased sex ratios in Eugenia may perhaps be due to a similar phenomenon. Casual observations on Eugenia simii did not suggest any habitat segregation between males and females,

something which would be difficult to determine in some of the other species owing to rarity of individuals in any one plant community. There is a need for more detailed demographic and experimental data on sex ratio variation in Eugenia.

The preponderance of male flowering specimens in herbaria may not always be an indication of a male-biased sex ratio in the natural populations of a species. The differential collecting of specimens from more floriferous (and consequently more attractive) male plants could also result in a skewed sex ratio among herbarium collections. This has undoubtedly also played a role in species of Eugenia, although it has already been pointed out that females are at least occasionally just as floriferous as males. In many species of Eugenia fruiting specimens (usually immature) are well represented or predominant in herbaria. This could be explained by the fact that the developing fruits remain on the trees for a much longer period than the flowers, hence the chance of collecting fruiting material is considerably increased.

4.6 Evolution of functional dioecy in Eugenia

It has been suggested that dioecism in seed plants has evolved by at least five distinct evolutionary pathways, viz. directly from hermaphroditism and through androdioecy, gynodioecy, monoecy and heterostyly (Bawa 1980; Ross 1980, 1982). The possible evolutionary pathway to dioecy in the native species of Eugenia is uncertain. Outside Africa only hermaphrodite flowers are known in Eugenia. It has therefore been taken for granted that the hermaphrodite state is the original one from which the dioecious species were derived. Authors have frequently indicated that inbreeding depression is usually necessary for the evolution of dioecy from hermaphroditism (e.g. Charlesworth & Charlesworth 1978, 1979; see also Baker 1959; Bawa & Opler 1975).

Unfortunately very little seems to be known about inbreeding depression and compatibility in the hermaphroditic species of Eugenia. Yet Sobrevila & Arroyo (1982) reported self-incompatibility in a claimed species of Eugenia from the neotropics. It should be stressed that a fair knowledge of breeding systems in Eugenia in the whole of Africa and elsewhere is essential to give a proper evaluation of the possible evolutionary pathways involved in the species studied.

On the basis of the present account, evidence for a possible evolutionary pathway from hermaphroditism to dioecy via gynodioecy does not appear particularly strong, but it is still plausible. Although subdioecious plants of this pathway are characterized by well differentiated females which seldom or never have any pollen (Ross 1980), a few cases are known in which the females retain non-functional stamens (Carlquist 1966; Young 1972). If gynodioecy was the pathway in Eugenia, then the male flowers would represent hermaphrodite flowers which through a reduction of seed set have come to function exclusively as males. Reduction of seed set on hermaphrodites has been described as a gradual process (Lloyd 1976; Ross 1980). Therefore one may expect to find an occasional variation in the degree of ovary development in functional males. Although by no means conspicuous, this is indeed the case in Eugenia where the ovules and style may be either rudimentary or apparently absent in male flowers. However, presently no southern African species of Eugenia display gynodioecy, but this may be because the evolutionary endpoint to dioecy via unstable gynodioecy has perhaps already been attained. Of particular significance may be the reports that both morphologically male and morphologically hermaphrodite flowers are very rarely present on the same plant in some African species of Eugenia to the north of our area (Amshoff 1958; White 1978). However, these

reports need confirmation because they are apparently based mainly on casual observations in the course of taxonomic revisions. We have for example noticed that a morphologically hermaphrodite flower may occasionally lose a style through predation or other damage and could then easily be confused with male flowers, particularly in herbarium specimens.

The sexual state of Saurauia veraguensis (Dilleniaceae) has recently been described by Haber & Bawa (1984) and is virtually identical to the condition in southern African species of Eugenia. These authors suggest that functional dioecy in Saurauia may have evolved via androdioecy or perhaps gynodioecy. The observed rarity of androdioecy (Lloyd 1975; Charlesworth & Charlesworth 1978) suggests that it is probably not an important pathway in the evolution of dioecy (also see Charlesworth 1984). The rarity or absence of androdioecy has been explained by certain limitations imposed on the transmittance of the necessary controlling genes in a natural hermaphrodite population (Lloyd 1975; Charlesworth & Charlesworth 1978; Charlesworth 1984). However, it has also been speculated that androdioecy could be maintained in outcrossing populations under conditions of a greater pollen production in the males resulting in pollinator mediated sexual selection (Bawa 1980; Bawa & Beach 1981; Beach 1981; Haber & Bawa 1984).

The presence of fertile pollen in hermaphrodite flowers of Eugenia in Africa may lend some support for a possible evolutionary pathway via androdioecy. It is difficult to interpret the significance of the very low numbers of 'sterile' grains which germinated in Saurauia veraguensis (Haber & Bawa 1984), Eugenia (this study; although origin of grains suspect) Pimento dioica (Chapman 1964) and Thalictrum polygamum (Kuhn 1939; Kaplan & Mulcahy 1971). Could the germinated grains perhaps represent an incipient stage in the evolution of in=

viable food grains? The few suspected foreign male-type grains noticed among sterile grains in Eugenia obtained from unbagged female flowers could be of considerable importance if it can be shown in future studies that male (fertile) grains may in fact sometimes be pro= duced by females.

In their discussion of dioecy in Saurauia, Haber & Bawa (1984) did not mention another plausible pathway, viz. the direct evolution of dioecy from hermaphroditism (Ross 1982). Charlesworth & Charlesworth (1978) argued on a priori reasoning that the direct evolution of dioecy from hermaphroditism is extremely unlikely because at least two gene mutations (c.f. Lewis 1942; Westergaard 1958; Charlesworth 1984) are deemed necessary. Ross (1982), however, presented some evidence sug= gesting the existence of a direct pathway without any gynodioecious intermediate stage (see also Bawa 1980). It is suggested that the latter pathway as well as the ones via gynodioecy and androdioecy could have been involved in the evolution of dioecy in the native species of Eugenia . This should be explored further in future studies.

The switch to morphological androdioecism and functional dioecism in both major groups of Eugenia in southern Africa is intriguing. Van Wyk & Botha (1984) do not consider species groups X and Y to be closely related and proposed that the groups may even constitute two separate genera. The distinctness of groups X and Y is also supported by the complete lack of putative hybrids between the two groups, despite the fact that species from both groups often grow together in the field. Evidence has been presented above, which indicate that a dioecious sex= ual state comparable to the one in Eugenia, also prevails among a number of species with pollen flowers in various other families. It therefore appears quite likely that a similar kind of sexual system could have evolved independently in groups X and Y. Such an evolutionary

development is likely to have arisen in response to the same or a very similar set of selective pressures. The questions as to the kind of selective pressures involved and why this rather unusual type of functional dioecy in Eugenia has only evolved in African species (consisting of two distinct supraspecific groups) offer considerable scope for future investigation.

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TABEL 1

List of southern African species of Eugenia covered by this paper - arranged according to supraspecific group.

GROUP	SPECIES
X	E. capensis (Eckl. & Zeyh.) Sond.
X	E. cf. mossambicensis Engl.
X	E. natalitia Sond.
X	E. simii Duemmer
X	E. umtamvunensis Van Wyk
Y	E. albanensis Sond.
Y	E. erythrophylla Strey
Y	E. pusilla Engl.
Y	E. verdoorniae Van Wyk
Y	E. woodii Duemmer
Y	E. zeyheri Harv.
Y	E. zuluensis Duemmer
Y	E. sp. A [a]
Y	E. sp. B [a]
Y	E. sp. C [a]

[a] Undescribed species; vouchers supplied in Van Wyk & Botha (1984)

TABLE 2.

Fruit set in UR population of *E. simii*

	Total no. of flowers bagged	No. of fruits	Fruit set (%)
Female plants			
1	116	72	66
2	45	15	33
3	58	13	22
Male plants			
1	52	0	0
2	45	0	0
3	33	0	0

TABLE 3

Sex ratios in populations of E. simii

Population	No. of males	No. of females	No. not flowering	Ratio (female:male)
Oribi Gorge	95	66	43	* 1 : 1.5
Uvongo River	7	7	3	1 : 1
Umtamvuna River	21	19	17	1 : 1.1

* $P < 0.05$ $X^2 = 5.2$

TABLE 4

Sorting of all fertile collections representing six species of *Eugenia* in the National Herbarium (PRE) according to sexual state.

SPECIES	NUMBER OF SPECIMENS		
	FLOWERING		FRUITING
	MALE	FEMALE	
E. albanensis	9	2	1
E. capensis	21	8	17
E. natalitia	18	15	34
E. woodii	13	3	14
E. zeyheri	9	3	5
E. zuluensis	2	0	3

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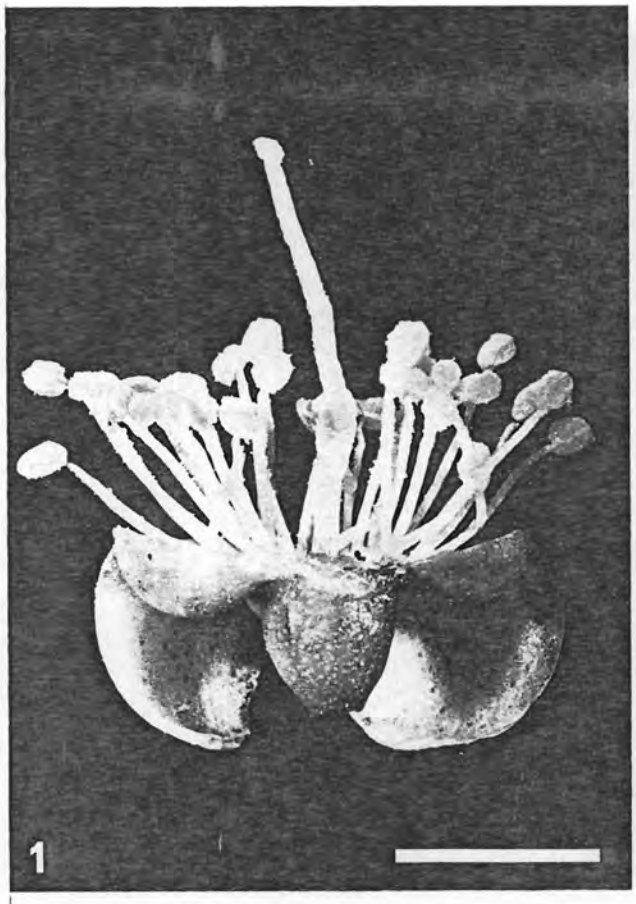
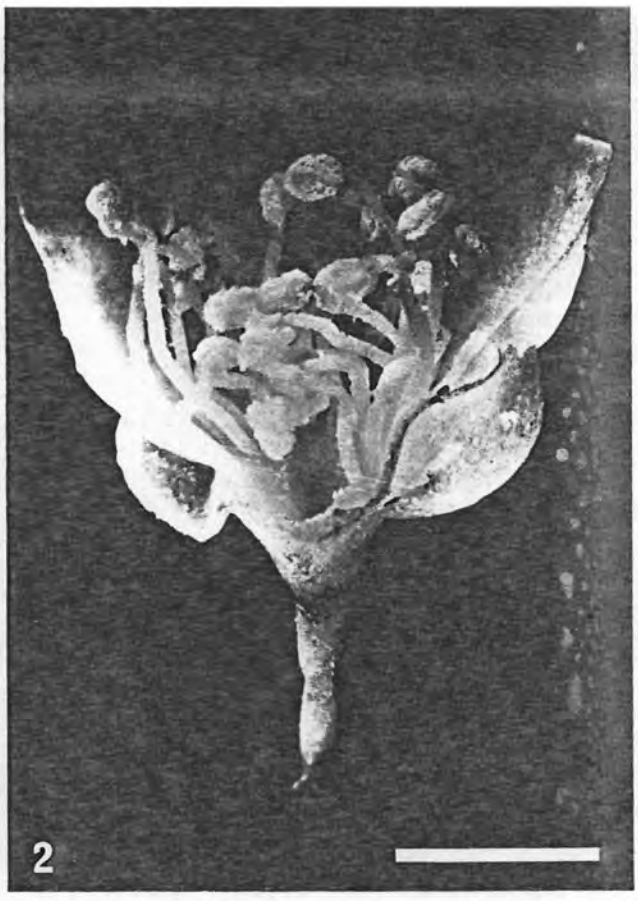
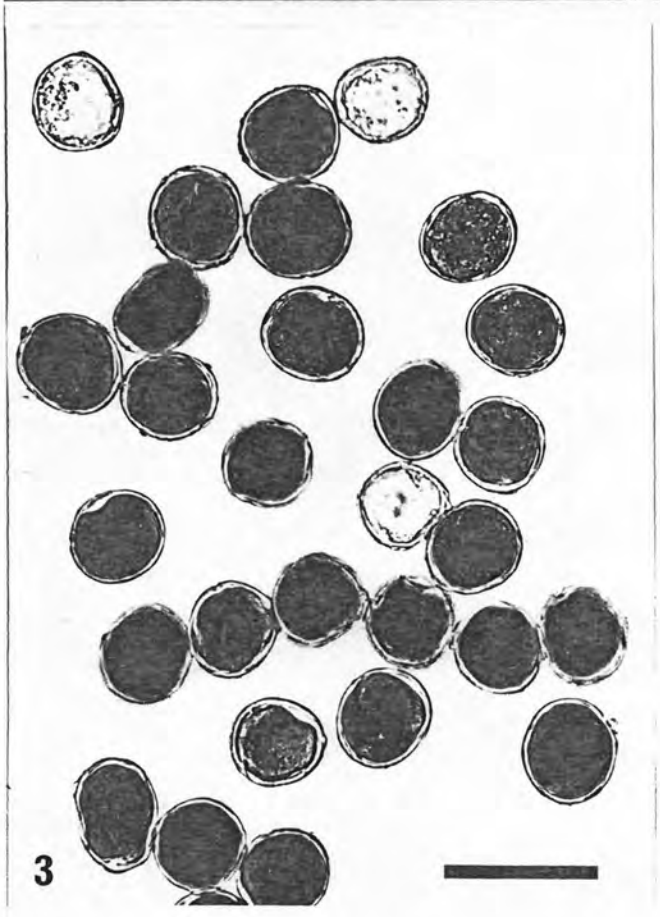
CAPTIONS FOR FIGURES

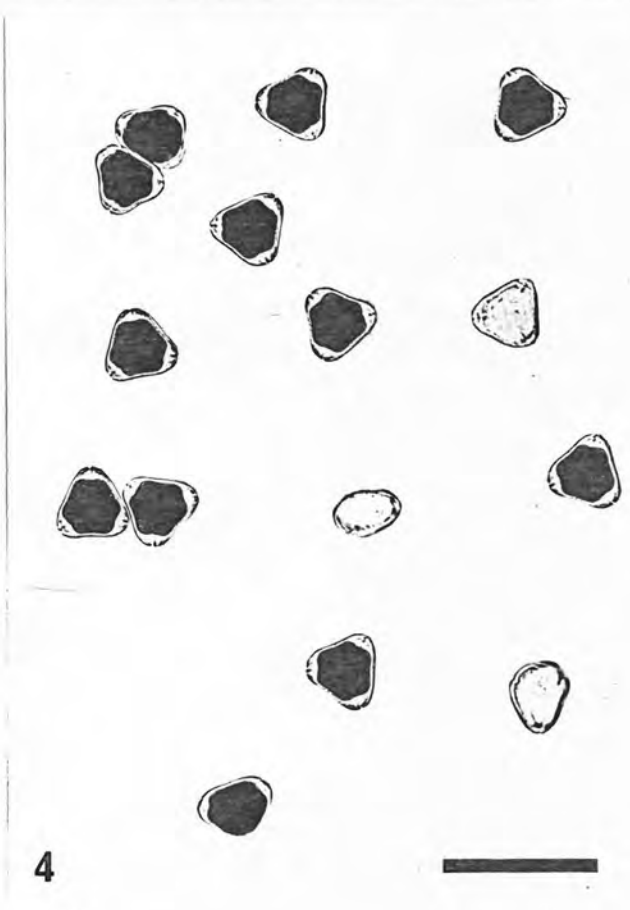
FIGURES 1 - 4. Flowers and pollen grains of Eugenia. 1 & 2. E. simii. - 1. Structurally hermaphrodite but functionally female flower. - 2. Male flower partly dissected to show the cup-shaped hypanthium and absence of a style. - 3. E. natalitia, stained pollen from female flower showing three aborted grains. - 4. E. woodii, stained pollen from male flower showing three aborted grains. Scale line = 5 mm in Figures 1 & 2 and 40µm in Figures 3 & 4.

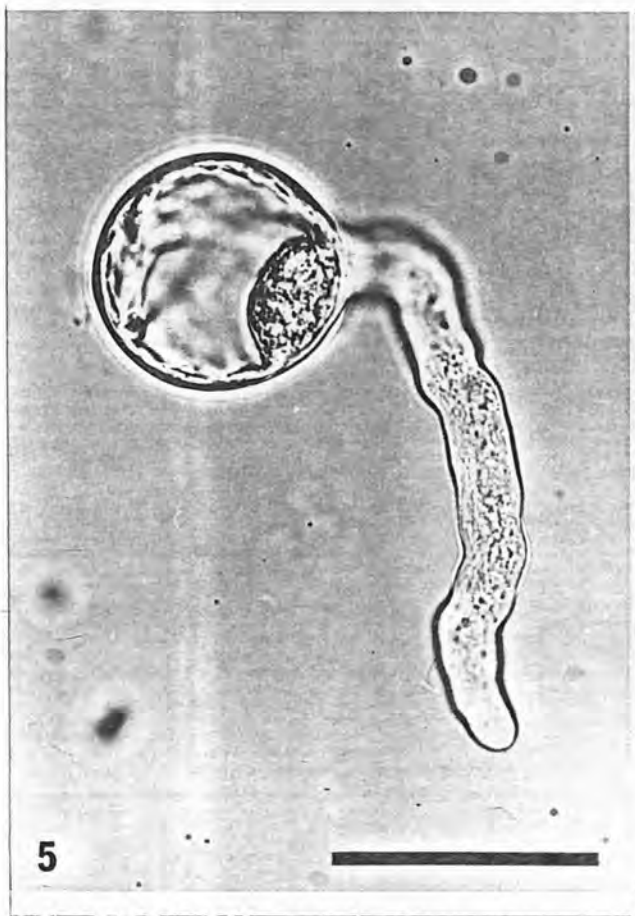
FIGURES 5 - 8. Germination of pollen grains in Eugenia. - 5. E. natalitia, in vitro germinating pollen grain from female flower (a very rare phenomenon). - 6. E. woodii, in vitro germinating pollen grains from male flower. 7 & 8. E. simii, in vivo pollen germination. - 7. Part of a squashed style of an open-pollinated female flower showing numerous pollen tubes with plugs of callose under ultraviolet light. - 8. Squashed stigma of open-pollinated female flower showing numerous fluorescent pollen tubes from small grains of male flowers but lack of pollen tubes from the large spherical grains (some arrowed) from female flowers. Scale line = 50µm in Figure 5 and 100µm in Figures 6 - 8.







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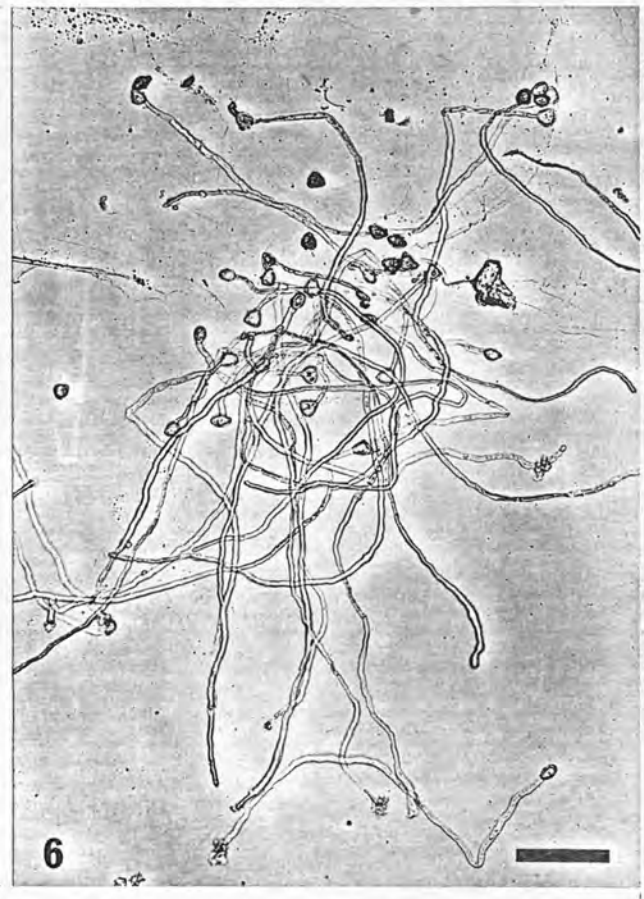
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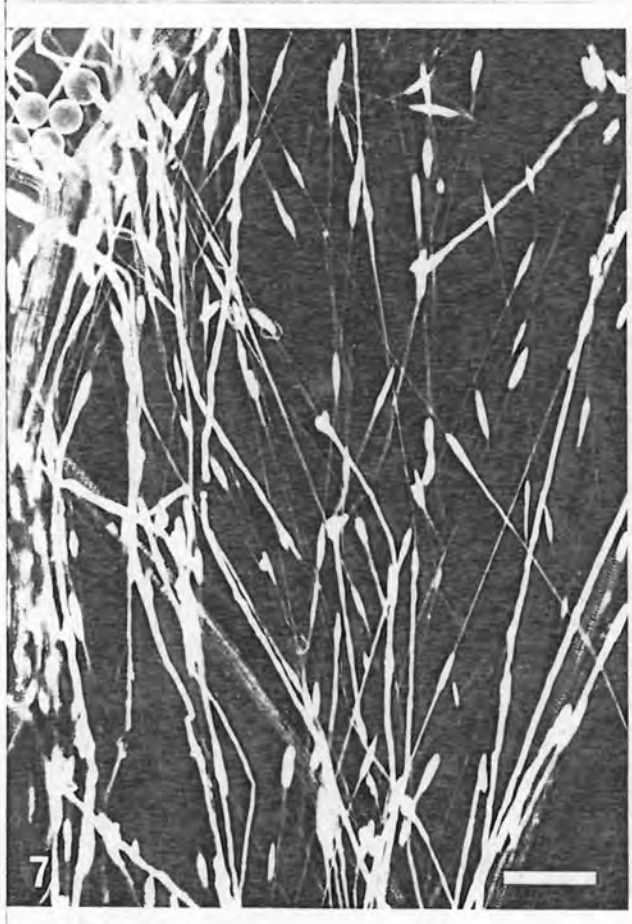
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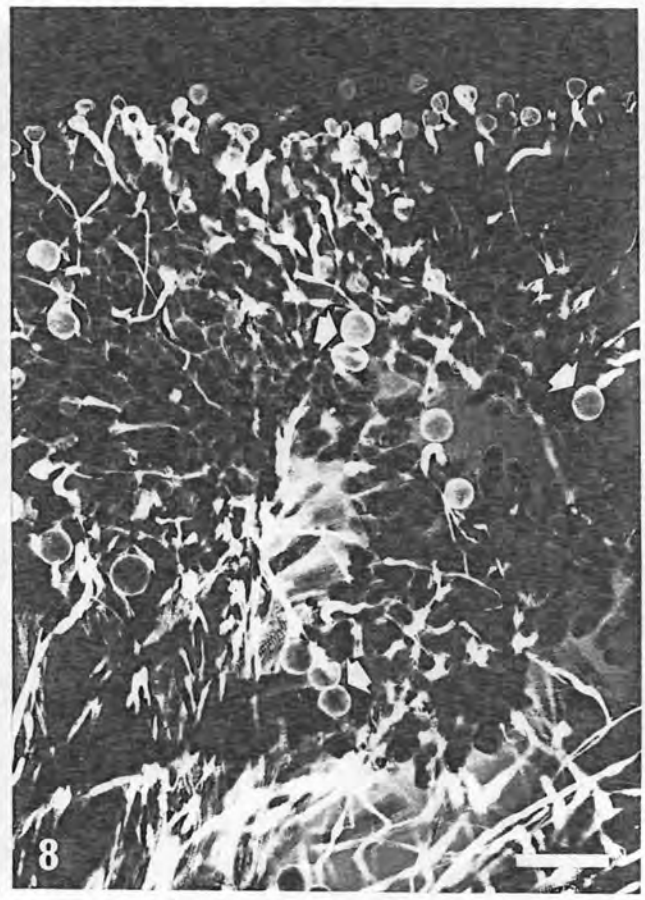
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CHAPTER 10

GENERAL DISCUSSION

CHAPTER 10

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10.1 INTRODUCTION

In this chapter the taxonomic significance of the contributions presented in the preceding chapters will be emphasized through a synthesis of the main conclusions. The information presented in Van Wyk (1978) and the papers included in this thesis, by no means represent all results obtained up to now. Characters of the inflorescence, flowers and fruits have only briefly been alluded to in Chapter 9, while various other observations have not yet been published. These observations will receive more attention in forthcoming publications. Some new evidence will also be briefly mentioned below and in Chapter 11.

In most of the preceding papers attention was primarily given to the merit and taxonomic status of the two groups of species, X and Y, first revealed by anatomical evidence of the leaf and stem. As a basis for the delimitation of the species, the classification proposed by Van Wyk (1978) was used. Extensive field-work has subsequently necessitated a few changes and additions. Observations during field-work have been the decisive factor for the recognition of taxa within groups X and Y. Delimitation of the taxa was initially based primarily on the gestalt perceived from the mainly vegetative appearance of the plants in the field. Previously authors have already recognized some of these taxa from herbarium specimens. Type specimens of most names applying to southern African taxa were studied to select existing validly published names to refer to the various groups. This a priori approach was deemed necessary to ensure a representative sampling of the major variations. The delimitation of the predetermined taxa was subsequently subjected to critical evaluation by analysing the evidence forthcoming from the various studies. An implication of this approach was that the rank rather than the delimitation of the taxa becomes one of the major issues requiring judgement. With the taxa provisionally circumscribed, more attention has also been given to speculations on their possible interrelationship. In this chapter some of the shortcomings and limitations of the work to date will also be mentioned. Finally the main features of a proposed new classification will be compared with existing alternative systems.

10.2 SUPRASPECIFIC TAXONOMY

The delimitation of the two supraspecific groups proposed by Van Wyk (1978) has received convincing support from subsequent studies. Besides the anatomical evidence on which it was introduced (Van Wyk 1978; Van Wyk *et al.* 1980; page 76) the subdivision is reinforced by the structure of the stomata (Van Wyk *et al.* 1982; page 5), seed (Van Wyk 1980; page 34; Van Wyk & Botha 1984; page 39) bark (Van Wyk 1985; page 98) and although not yet published in detail, inflorescence position and fruit morphology (Van Wyk & Lowrey, in press; page 133). Perhaps the most surprising discovery was the marked differences shown by groups X and Y in the structure and ontogeny of the seeds. On the other hand no obvious support for the supraspecific groups is provided by the foliar organography (excluding leaf colour) (Du Plessis & Van Wyk 1982; page 22), wood anatomy (Van Wyk *et al.* 1983; page 58), flower and pollen morphology (Van Wyk & Dedekind 1985; page 124). In fresh foliage leaves the lower lamina surface is often light green with distinct secretory cavities in group X and whitish green with the secretory cavities obscure in group Y. The latter feature and bark structure proved very useful to distinguish between sterile members of groups X and Y in the field. For determining the groups among sterile herbarium material the most reliable method is to establish the position of the first-formed stem periderm in the young twigs (Van Wyk *et al.* 1980; page 76). It is significant that the sets of differentiating characters show complete correlation within groups and discontinuity between groups. There can therefore be no doubt that groups X and Y are, at least in southern Africa, two very distinct and apparently natural categories.

This fact led to the question of the formal taxonomic status of the two groups to be considered. Particularly seed structure and seed ontogeny are quite different between the groups (Van Wyk & Botha 1984; page 39) and in view of the considerable taxonomic significance attributed in the past to seed characters in the Myrtoideae, it was anticipated that these features may shed light on the question of ranking. However, the lack of comparative published evidence for *Eugenia* L. and eugenioid genera from other parts of the world makes

meaningful comparisons impossible. In fact, the lack of comparative data has been a constant source of frustration throughout these studies.

From the very scanty available information, Van Wyk & Botha (1984; page 39) nevertheless suggested that on the basis of seed structure, species group X seems to be most closely related to some mainly New World species of *Eugenia*. A subsequent study of material from the American tropics (unpublished data) confirmed this statement. Van Wyk & Botha (1984; page 39) also provisionally concluded that species group Y does not seem to be closely related to any groups outside Africa, although we suggested a detailed comparison with especially American eugenioid genera and the Old World genus *Jossinia* Comm. ex DC. (relegated to the synonymy of *Eugenia s.str.* by modern authors). Since then I also had the opportunity to study material that some authors would have placed in *Jossinia*, from Sri Lanka, Madagascar and the Mascarene Islands. The still unpublished results strongly suggest a link between group Y and *Jossinia*. They have an almost identical pachychalazal seed-coat, although an extended hilum has thus far been found only in the African members. In addition, *Jossinia* usually appears to be multi-ovulate compared with the usually two to four ovules per locule in group Y. A peculiarity of the *Jossinia* species which has not yet been recorded in the native species of *Eugenia* (and as far as I have ascertained also not the American members) is the presence of foliar sclereids in the palisade layer. The first-formed periderm in the stems of *Jossinia* usually originates in the deeper layers of the cortex thereby recalling the deep-seated (primary external phloem) periderm in group Y. However, the lack of an extraxylary ring of primary phloem fibres sometimes makes it difficult to establish whether the first-formed periderm originates in the cortex or the primary external phloem. A ring of primary phloem fibres is usually present in most of the native species of *Eugenia*.

As pointed out by Van Wyk & Botha (1984; page 39), we are rather reluctant to merely accept the reduction of *Jossinia* to the synonymy of *Eugenia*. Considering the evidence now available, the possible reinstatement of *Jossinia* should be seriously considered. Van Wyk & Botha (1984; page 39) provisionally proposed that species group Y be allocated generic rank. Should group Y be considered a separate genus, uniform standards would require a reinstatement of *Jossinia*, whether or not group Y is assigned to this or any genus other than *Eugenia*. The implications of such a step would be far-reaching, particularly necessitating name changes for many Old World species of *Eugenia*.

Studies such as those on the southern African species should be extended to more members of *Eugenia s.str.* in both the New and Old World. Only then can valid conclusions as to generic limits be drawn. Many more observations are needed, particularly with respect to comparative anatomy and seed structure.

At this stage a major limitation of the present work on *Eugenia*, namely its restricted geographical scope, should be identified. Within the confines of southern Africa there is a clear distinction between groups X and Y. Whether this will hold firm when species from the rest of Africa and other parts of the world are included, remains to be determined. Although very limited African material from outside the FSA region has been studied, as yet there is no apparent break-down of the groups. In fact, species group Y seems to be centred in southern Africa, with *E. woodii* Duemmer and perhaps *E. albanensis* Sond. the only known members of the group spreading into the FZ region. More worrying, however, is that the distinction may break down in the neotropics. I am now of the opinion that the tissues forming the dark-coloured lateral extensions (areolae) in seed type X (see Figure 9; page 42) are homologous to the seed-coat of seed type Y, excluding the more lightly coloured radicular depression (see Figure 10E; page 43). Hence the seed-coat in seed type X is partly derived from chalazal tissue. One or two South American taxa were found to have seeds with the areolae are so well developed that only a small area of the seed-coat around the micropyle seems to be derived from the integuments. This approaches the condition in seed type Y and suggests that seed type X could be an intermediate stage towards the eventual evolvement of a pachychalazal seed resembling the former type. On the other hand, parallel evolution is probably widespread among eugenioid genera and this further complicates comparative work on the group. It would therefore be premature to pass final judgement on the formal taxonomic status of groups X and Y. In the meantime both groups are maintained as informal supraspecific categories.

10.3 SPECIFIC AND INFRASPECIFIC TAXONOMY

When work on *Eugenia* in southern Africa commenced about 10 years ago, the principal difficulty in the delimitation of the infrageneric taxa (as defined originally mainly by differences observed in the field) was the close resemblance between specimens in the herbarium. Some taxa betrayed their artificiality by an uncommonly wide range of variability and by vague and disputable boundary lines. However, the discovery of the two supraspecific groups facilitates the removal of discordant elements from such taxa. Since then the delimitation of the infrageneric taxa has not presented any major difficulties. Varying degrees of support for the proposed delimitations came from various sources. Noteworthy perhaps is the numerical studies employing 100 anatomical (Van Wyk 1978) and 20 leaf organographical characters (Du Plessis & Van Wyk 1982; page 22). On the other hand, some aspects such as wood anatomy (Van Wyk *et al.* 1983; page 58) and pollen morphology (Van Wyk & Dedekind 1985; page 124) were not very useful in this regard, but this was not unexpected in a family notorious for a paucity of taxonomically significant evidence from these sources.

Whether to allocate specific or subspecific rank to the infrageneric taxa turned out to be difficult, particularly

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TABLE 1.—Proposed new classification of the species of *Eugenia* in the FSA region compared with the classification of Duemmer (1912) and taxa proposed by White (1977 & 1978)

DUEMMER (1912)	WHITE (1977 & 1978)*	PROPOSED NEW CLASSIFICATION
		GROUP X
Eugenia capensis (Eckl. & Zeyh.) Sond. ≡ *Memecylon capense* Eckl. & Zeyh. Var. *capensis* Var. *major* Sond.	*Eugenia capensis* (Eckl. & Zeyh.) Sond. ≡ *Memecylon capense* Eckl. & Zeyh. Subsp. *capensis* = *E. capensis* var. *major* Sond. = *Myrtus capensis* Harv. non *E. capensis* (Eckl. & Zeyh.) Sond.	*Eugenia capensis* (Eckl. & Zeyh.) Sond. ≡ *Memecylon capense* Eckl. & Zeyh. Subsp. *capensis* = *E. capensis* var. *major* Sond. = *Myrtus capensis* Harv. non *E. capensis* (Eckl. & Zeyh.) Sond.
E. gueinzii Sond.	Subsp. *gueinzii* (Sond.) F. White ≡ *E. gueinzii* Sond.	Subsp. *gueinzii* (Sond.) F. White ≡ *E. gueinzii* Sond.
		Subsp. A = *E.* cf. *mossambicensis* Engl. sensu Van Wyk
E. natalitia Sond.	Subsp. *natalitia* (Sond.) F. White. ≡ *E. natalitia* Sond. = *E. woodii* Duemmer = *E. zuluensis* Duemmer = *E. rudatisii* Engl. & v. Brehm.	*E. natalitia* Sond. = *?E. natalitia* var. *medleyiana* Engl. & v. Brehm. ≡ *E. capensis* subsp. *natalitia* (Sond.) F. White *p.p.* = *E. rudatisii* Engl. & v. Brehm.
E. simii Duemmer	Subsp. *simii* (Duemmer) F. White) ≡ *E. simii* Duemmer	*E. simii* Duemmer ≡ *E. capensis* subsp. *simii* (Duemmer) F. White
		E. umtamvunensis Van Wyk
		GROUP Y
E. albanensis Sond.	Subsp. *albanensis* (Sond.) F. White ≡ *E. albanensis* Sond.	*E. albanensis* Sond. ≡ *E. capensis* subsp. *albanensis* (Sond.) F. White
E. woodii Duemmer		*E. woodii* Duemmer Subsp. *woodii* = *E. capensis* subsp. *natalitia* (Sond.) F. White *p.p.*
		Subsp. A = *?E. capensis* susbp. *natalitia* (Sond.) F. White *p.p.*
E. zuluensis Duemmer		*E. zuluensis* Duemmer = *E. capensis* subsp. *natalitia* (Sond.) F. White *p.p.*
E. zeyheri (Harv.) Harv. ≡ *Myrtus zeyheri* Harv. Var. *zeyheri* Var. *angustifolia* Duemmer	subsp. *zeyheri* (Harv.) F. White ≡ *Myrtus zeyheri* Harv. ≡ *E. zeyheri* (Harv.) Harv.	*E. zeyheri* (Harv.) Harv. ≡ *Myrtus zeyheri* Harv. = *? E. zeyheri* var. *angustifolia* Duemmer ≡ *E. capensis* subsp. *zeyheri* (Harv.) F. White
	E. erythrophylla Strey	*E. erythrophylla* Strey
E. pusilla N.E. Br. Var. *pusilla* Var. *latior* Duemmer		*E. pusilla* N.E. Br.
		E. verdoorniae Van Wyk
		E. sp. A
		E. sp. B
		E. sp. C
		TAXON INSUFFICIENTLY KNOWN
		E. pusilla var. *latior* Duemmer
		EXCLUDED SPECIES
E. incerta Duemmer		*E. incerta* Duemmer = exotic species of unknown origin
E. cordata (Hochst. ex Krauss) Laws.		*E. cordata* (Hochst. ex Krauss) Laws. = *Syzygium*
E. gerrardii (Harv. ex Hook. f.) Sim		*E. gerrardii* (Harv. ex Hook. f.) Sim = *Syzygium*
E. fourcadei Duemmer		*E. fourcadei* Duemmer = *Syzygium*

* A formal revision covering the FSA region has not yet been published. This is a selection of proposed taxa and their synonyms applicable to the FSA region.

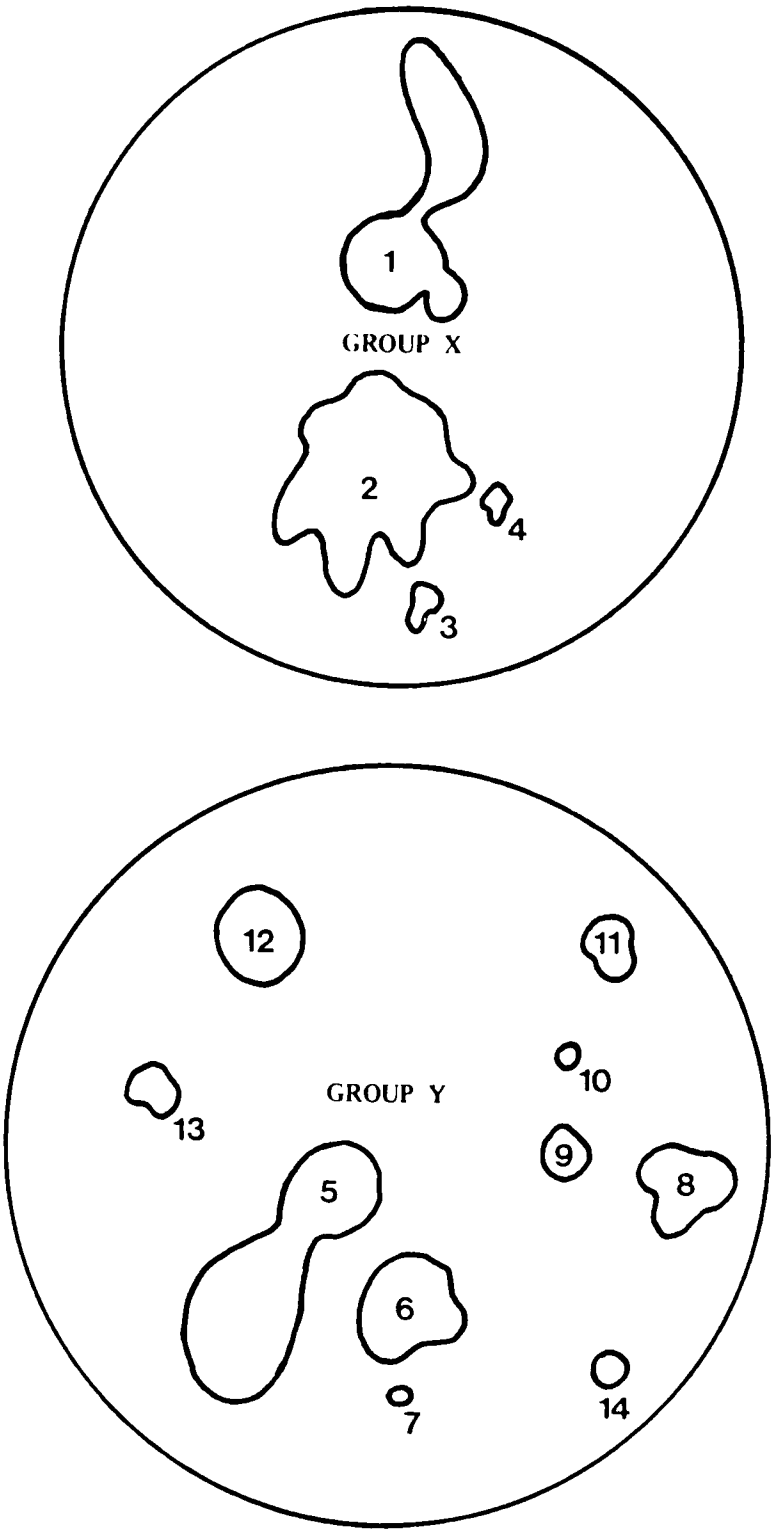

FIG. 1—Representation of the possible relationships between the species of *Eugenia* in the FSA region. The size of each 'bubble' is roughly proportional to the geographical area covered by the species, the evenness of outline to the infraspecific variability and the distance between species reflects on the degree of similarity. 1. *E. capensis*, 2. *E. natalitia*, 3. *E. simii*, 4. *E. umtamvunensis*, 5. *E. woodii*, 6. *E. albanensis*, 7. *E. pusilla*, 8. *E. zeyheri*, 9. *E.* sp. A, 10. *E.* sp. B, 11. *E. erythrophylla*, 12. *E. zuluensis*, 13. *E.* sp. C, 14. *E. verdoorniae*.

in species group X where the taxa are much more closely related than in group Y. For example, in group X, *E. capensis* and *E. natalitia* are quite distinct and to my mind deserve specific status. However, the differences between *E. simii* Duemmer, *E. umtamvunensis* Van Wyk and *E. natalitia* Sond. are relatively less pronounced and one could also treat these taxa as subspecies under *E. natalitia* (the oldest name). Between all these taxa variation is essentially discontinuous in regions where populations are sympatric or parapatric.

It should be appreciated that the 'magnitude' of diagnostic character states, at the species level, is smaller in *Eugenia* than in many other groups of plants. Diagnostic characters at all levels of the taxonomic hierarchy are scaled down in the Myrtoideae and this is to be accepted as an intrinsic feature of the group. It can be well imagined that a worker who has mostly dealt with groups where species differences are marked, may easily tend to lump together species when working on a taxon such as *Eugenia*. After all, the lumping of species is one of the more 'convenient' ways of dealing with a difficult group.

It is my conviction that the choice between specific and subspecific rank in *Eugenia* is very much a subjective one. In fact, for some taxa both choices would be acceptable to me. Hence I do not present a detailed rationale for my ranking decisions, but will content with brief notes on the subject under some of the critical taxa in Chapter 11. More important to me is the soundness of the delimitation of the taxa and also the most accurate conveyance of the possible evolutionary relationships. With subspecies this is particularly crucial because the subspecific name reflects on the latter issue.

A provisional (with regard to rank) classification of the species of *Eugenia* native to the FSA region is presented in Table 1, where it is compared with the classification of Duemmer (1912) and some of the taxa recognized by White (1977 & 1978). From a total of 14 species, five have not previously been recognized as separate taxa. Three of the new species are still undescribed and are referred to as *Eugenia* sp. A, B & C. *E. incerta* Duemmer, described from a cultivated plant, is an exotic species of unknown origin and is almost certainly known under another name in its country of origin. Keys to the species and notes on infraspecific taxa, diagnostic characters and geographical distribution are presented in the next chapter. A representation of the possible relationships between the taxa is suggested in Figure 1. I am fully aware of the criticism it may evoke because I dare present it without employing some kind of scientific method. It is, however, presented as a hypothesis with a challenge to put it to the test with so-called rigorous methods.

The following passage pertaining to the subspecies of *E. capensis* (Eckl. & Zeyh.) Sond. is quoted from the treatment of *Eugenia* in FZ (White 1978): *'Apart from some trifling differences in size, the flowers and fruits seem to be uniform. The subspecies differ chiefly in habit and habitat and in the shape, size and texture of their leaves. Although the differences between related subspecies are slight, and collectively their variation forms a continuum, they are almost entirely ecogeographically distinct.'* I can confirm that taxa belonging to group X (more so than in group Y) *tend* to be confined to specific habitats, e.g. *E. capensis* subsp. *capensis* on coastal dunes, *E. capensis* subsp. A on deep sandy soils in coastal and savanna regions, *E. natalitia* in coastal and inland forest areas and *E. simii* along water-courses. For group Y, *E. albanensis* is confined to grassland, *E. zuluensis* Duemmer is a subcanopy tree in mist belt forest and *E. woodii* Duemmer occurs in coastal and inland forest. Exceptions do occur, however, e.g. *E. erythrophylla* Strey, *E. verdoorniae* Van Wyk and *E.* sp. C are often sympatric in the forests of Pondoland and southern Natal. Taxa from both groups may also grow together, e.g. *E. woodii* and *E. natalitia* in particularly the forests of the Soutpansberg and Transvaal Drakensberg, and *E. albanensis* and *E. capensis* subsp. A in the coastal grassland of Maputaland. No possible hybrids have ever been encountered between sympatric species or any other pair of native species of *Eugenia*.

If my perception of White's reasoning is correct, he seems to consider the subspecies of *E. capensis* essentially equivalent to ecotypes. The differences between the species (in the sense of the present author) persisted when seed samples of different populations were grown under uniform conditions. This surely indicates genotypic differences and not environmental modifications. Gradual speciation through an ecotypic phase is generally accepted as one of the pathways for the realization of new species (e.g. Briggs & Walters 1984). It seems very likely that, particularly in group X, species might have proceeded through an ecotypic phase first, with the eventual gradual evolution of genetic or other isolating mechanisms. I can see no reason why related but distinct taxa occupying different habitats cannot be ranked as species, particularly when variation is essentially discontinuous and there are more differences than just leaf shape. Accidentally there are some derivatives, particularly of *E. natalitia*, which may be in the process of passing through the ecotypic phase (e.g. a riverine shrub along the Blyde River in the NE Transvaal). Because these sibling taxa still tend to intergrade with the putative parent species, I have not attempted to give them taxonomic status at this stage. In future subspecific status may perhaps be considered for such variations.

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CHAPTER 11

PROVISIONAL KEY TO THE SPECIES OF *EUGENIA* IN SOUTHERN AFRICA, WITH NOTES ON DIAGNOSTIC CHARACTERS, GEOGRAPHICAL DISTRIBUTION, TYPIFICATION AND SYNONYMY

CHAPTER 11

PROVISIONAL KEY TO THE SPECIES OF *EUGENIA* IN SOUTHERN AFRICA, WITH NOTES ON DIAGNOSTIC CHARACTERS, GEOGRAPHICAL DISTRIBUTION, TYPIFICATION AND SYNONYMY

11.1 INTRODUCTION

This chapter supplements the outline of a new classification of *Eugenia* in the FSA region proposed in Table 1, page 175 . Its aim is to serve as an introduction to the various taxa in anticipation of the formal revision which is now in preparation. To help convey my concept of the taxa, brief descriptions emphasizing diagnostic features are provided (11.3) together with three papers containing detailed descriptions of *E. verdoorniae* (Van Wyk 1980; page 201), *E. woodii* (Van Wyk 1982; page 207) and *E. umtamvunensis* (Van Wyk 1984; page 189). Also included are a popular scientific paper on *E. albanensis* (Van Wyk 1985; page 195), keys to the species (11.2), synonyms, type specimens, distributional data and the citation of representative herbarium specimens (all 11.3). In the synopsis of the names (11.3) only the publication in which a name first appeared, is cited. Type localities are given as published by the original author, unless I have seen the type specimen(s)—in which case the wording on the type sheet was recorded. The original spelling of place names was retained and orthographic errors were not corrected. The chapter is concluded with photographs of herbarium specimens representative of the various taxa (11.4).

I am trying to investigate type specimens of all the names applied to at least southern African material of *Eugenia*. Some specimens could hitherto not be traced, but those already seen are indicated by an exclamation mark. Fortunately the native species of *Eugenia* are not burdened by major nomenclatural problems. In this regard the present work has also benefitted from the recent contributions by White (1977 & 1978). It is nevertheless possible that some of the local species will prove to be identical with others which have been described previously from material collected from the north of the FSA region and vice versa. For example, *E. chirindensis* Bak. and *E. nyassensis* Engl. from the FZ region, may be conspecific with *E. natalitia* and/or *E. woodii*. It therefore seems necessary in future to undertake at least a cursory survey of all African representatives of the genus to establish and delimit the principal species and their patterns of distribution. Typification of some of the names proposed by particularly Engler (1899 & 1921) and Engler & Von Brehmer (1917) will probably involve an undue amount of study, mostly because of the destruction of the Myrtaceae in the Berlin Herbarium during World War II. I have not yet concerned myself with the lectotypification of names.

The species of *Eugenia* from the FSA region seem to be largely endemic. There is a high degree of endemism among the species occurring in the sandstone (Natal Group) region of southern Natal and Pondoland. Of the 10 species recorded in the latter region, six are endemic. Species which range to the north of the FSA region are *E. woodii, E. capensis* and probably also *E. albanensis* and *E. natalitia*.

In addition to the representative specimens supplied in this chapter, voucher specimens for most species are listed in many of the papers included in this thesis. The application of the name *E. zeyheri* to specimens listed in Van Wyk (1978) is no longer correct because of subsequent changes to the circumscription of this species (see 11.3.10). Specimens previously referred to as *E.* cf. *mossambicensis* are now included in *E. capensis* (Eckl. & Zeyh.) Sond. subsp. A. The abbreviations for herbaria cited below and elsewhere in this thesis are those recommended in Index Herbariorum, ed. 7 (1981). Discriptors used to indicate abundance and frequency are based on those proposed by Schmid (1982).

11.2 KEYS TO THE SPECIES OF *EUGENIA* IN THE FSA REGION

The following notes are presented to assist in the use of the keys. It is difficult to construct a satisfactory general key to the species and the identification of *Eugenia* material will not be easy for the casual student. There is a certain parallelism between different species, particularly in respect of leaf shape. The difficulties are increased by the vegetative uniformity that prevails throughout the genus. Features such as the orientation, texture, colour and lustre of leaves are often useful in field identification but are to a large extent lost in herbarium specimens. Even the folding of wilted leaves in plants exposed to drought conditions may be diagnostic. For example, the characteristic folding of wilted leaves in *E. albanensis* helps to separate the species from *E. zeyheri*. In the herbarium it is otherwise very difficult to distinguish between sterile specimens of these two species if the growth form

of the plants is unknown. Although floral morphology varies little from one species to another, it provides some useful diagnostic features. Characters of the structurally hermaphrodite (functionally female) flowers are taxonomically more significant but are rare in herbaria (for possible reasons see Van Wyk & Lowrey, page 133). Fruiting material is likewise rarely encountered.

It is practically impossible to construct a usable key for the identification of sterile herbarium specimens, because some of the reliable specific distinctions depend upon characters of the seeds, flowers and inflorescences (unless some anatomical characters are introduced). With the exception of distinctive species such as *E. capensis*, *E. verdoorniae*, *E. zuluensis* and *E.* sp. A, it is essential to establish whether specimens to be identified, belong to species groups X or Y. If fruiting material is not available for this purpose, an easy and reliable alternative is to establish the position of the first-formed stem periderm in freehand sections (see Van Wyk *et al.* 1980; page 76).

The comprehensive specific key below (11.2.1) may not be very practical for identification in the herbarium. It will hopefully, however, largely summarize the characters of the species in easily comprehensible form. The key is mainly based on morphological characters, supplemented by particularly significant anatomical evidence. The shape of the hypanthium in structurally hermaphrodite flowers (obconical vs. globose-obconical) is only reliable if determined in fresh or spirit material. The comprehensive key is supplemented by two simplified pictorial keys (11.2.2 & 11.2.3). These are based on a selection of the more significant diagnostic characters.

Many of the species are confined to a well defined geographical area and/or habitat. This is of considerable aid in identification and has therefore been incorporated in the keys. No provision is made for variations which are very rare and hence unlikely to be encountered. A key to all possible forms of all species will be unwieldy and equivocal, thereby defeating its own purpose. Some experience with the group may be essential to identify aberrant and sterile specimens. Not included in the keys is *E. uniflora* L., an exotic species cultivated for ornamental purposes and now naturalized in places along the Natal coast.

11.2.1 COMPREHENSIVE KEY TO THE SPECIES OF *EUGENIA* IN THE FSA REGION

1 Seed from single seeded fruits more or less reniform or oblong-globose; testa tends to be exotestal, relatively thin (*ca.* 0,25 mm), with two dark brown areolae connected by a narrow isthmus visible on the inner surface; hilum linear-elliptic and not expanded; embryo with all the free surfaces abundantly dotted with secretory cavities; boles with bark type X (see page 101); lower lamina surface in fresh leaves usually light green and conspicuously gland-dotted; dried leaves usually not conspicuously discolourous; young leaves glabrous or sparingly pubescent; flowers white, very rarely tinged with pink, borne predominantly in the axils of the previous season's growth (ramiflorous); usually fasciculate in brachyblasts or in short racemes which do not develop as leafy shoots, rarely solitary in the basal bracteate axils of new shoots, never in cymules; ripe fruits purplish-black with whitish flesh; stems with the first-formed periderm originating subepidermally in the cortex; leaves with stomatal type X (see page 9) . . . . . **A. SPECIES GROUP X**

2 Structurally hermaphrodite flowers with the hypanthium obconical ('infundibular'); stigma flattened and conspicuously expanded, bi-fid, orbicular or elliptic in outline; interstaminal area surrounding the style usually conspicuously convex; young branchlets with a rather dense and fairly persistent indumentum of short erect hairs, occasionally more or less glabrous—particularly in suffrutices; leaf blades with the primary vein often not reaching the apex but branching some distance before to join the marginal vein (see Figure 6b & c, page 26); flowers axillary in 1–10(15)-flowered fascicles, very rarely in short axillary racemes, true solitary flowers not observed; pedicels usually (4)8–16 (18) mm long; dried flowers with the hypanthium and petals not conspicuously gland-dotted (except in suffrutices); seeds oblong-globose with the testa tending to adhere to the pericarp; mature bole bark with phellem 1,0–2,5 mm thick; stem with the extraxylary cylinder of fibres (pericycle) usually poorly developed or absent; small trees and shrubs on coastal dunes, or grassland rhizomatous suffrutices in coastal and inland forest and savannah regions . . . . . 11.3.1. *E. capensis*

2 Structurally hermaphrodite flowers with the hypanthium globose-obconical ('campanulate'); stigma slightly capitate or punctiform; interstaminal area surrounding the style plane or slightly convex; young branchlets glabrous or very sparingly appressed pubescent, soon becoming glabrous; leaf blades with the primary vein terminating at the apex (see Figure 6a, page 26); flowers axillary in 1–8(12)-flowered fascicles, occasionally in short axillary racemes or solitary at the lower bracteate nodes of new leafy shoots; pedicels usually (3)4–8(12) mm long; dried flowers with the hypanthium and petals usually conspicuously gland-dotted; seeds more or less reniform with the testa free from the pericarp; mature bole bark with phellem 0,3–0,6(0,8) mm thick; stems with the extraxylary cylinder of fibres (pericycle) usually well developed and occasionally almost continuous.

3 Branchlets relatively thick and stout, dark rusty-brown becoming grey with age, occasionally with rather prominent irregular longitudinal ribs; leaves thick and coriaceous, apex obtuse, rounded or occasionally shortly and bluntly acute; flowers usually in conspicuous brachyblasts up to 6 mm long, short axillary racemes (anauxotelic inflorescences) not recorded; flowers sessile or with pedicels up to 4(6) mm long; pericarp with maximum thickness (4)6–12 mm; mature bole bark with the inner bark (3)5–8(10) mm wide; slash dark reddish-brown; medium sized trees, rarely shrubs, in forest margins; endemic to the sandstone region of southern Natal and Pondoland . . . . . 11.3.4. *E. umtamvunensis*

3 Branchlets relatively thin and slender, light or rarely dark brown becoming grey with age, not conspicuously ribbed; leaves thinly coriaceous, apex acute, caudate-acute or acuminate; brachyblasts when present never conspicuous, short axillary racemes often present, pedicels usually (3)4–8(12) mm long; pericarp with maximum thickness 1–2 mm; mature bole bark with the inner bark (0,8)1–2(2,5) mm wide; slash creamish- or pinkish-brown, rarely dark reddish-brown.

4 Leaves narrowly oblanceolate or narrowly elliptic, apex acute, never with a jutting point; margin entire; internodes of normal growth (4)6–10(20) mm long; much-branched shrubs, nearly always confined to the banks and islands of rivers; endemic to the sandstone region of southern Natal and Pondoland . . . . . 11.3.3. *E. simii*

4 Leaves widely elliptic, elliptic or rarely narrowly elliptic or oblanceolate, apex caudate-acute, acute or bluntly acuminate, occasionally with a jutting point; margin entire or rarely weakly crenate; internodes of normal growth (6)15–25(35) mm long; medium sized trees, rarely shrubs, mainly confined to forest, rarely with riverine forms; recorded from Transkei (including Pondoland), Natal, Swaziland, Transvaal, Venda and probably ranging into the FZ region . . . . . 11.3.2. *E. natalitia*

1 Seed from single seeded fruits more or less globose; testa mesotestal, relatively thick (*ca.* 0,75 mm), with a whitish coloured depression on the inner surface in the micropylar region; hilum expanded and occupying about one hemisphere; embryo with secretory cavities absent or with a few scattered ones mainly in the vicinity of the radicular protuberance; boles with bark type Y (see page 102); lower lamina surface usually whitish-green and not conspicuously gland-dotted; dried leaves occasionally conspicuously discolourous; young leaves almost glabrous to densely pubescent; flowers white often tinged with pink, borne predominantly in the axils of the new season's growth; usually solitary in the lower bracteate axils of leafy shoots, occasionally in short racemes with restricted growth, or in mainly 3-flowered cymules, never fasciculate in brachyblasts; ripe fruits bright red (rarely creamish-orange in *E. albanensis*) with yellowish flesh; stems with the first-formed periderm originating in the primary external phloem; leaves with stomatal type Y (see page 11) . . . . . **B. SPECIES GROUP Y**

5 Rhizomatous suffrutices not exceeding 0,4 m in height, forming clones in grassland.

6 Leaves linear lanceolate or linear elliptic, 2–3(4) mm wide; bracteoles filiform; recorded from the Piet Retief district *ca.* 1911 and not re-collected since then . . . . . 11.3.7. *E. pusilla*

6 Leaves narrowly elliptic to elliptic or narrowly oblanceolate to oblanceolate (spathulate), (5)10–20 mm wide; bracteoles lanceolate acute, occasionally foliaceous; ranging from the eastern Cape to the south of Mozambique and with isolated populations in the eastern Transvaal . . . . . 11.3.5. *E. albanensis*

5 Trees or shrubs confined to forest or other tree-dominated vegetation types.

7 Leaves with the midrib markedly elevated into a narrow median ridge on the upper lamina surface; mature bole bark with a conspicuous pseudorhytidome, phellem with n-phelloids only (see page 99); an undercanopy tree of mistbelt forest; common in the Natal midlands and the extreme northern parts of Transkei, rare in the north-eastern Transvaal . . . . . 11.3.11. *E. zuluensis*

7 Leaves with the midrib channelled between slightly convex ridges, narrowly impressed, slightly concave or more or less plane on the upper lamina surface; mature bole bark with a pseudorhytidome inconspicuous or absent, phellem with both p- and n-phelloids usually present (see page 99).

8 Structurally hermaphrodite flowers with the hypanthium densely pubescent; flowers pedicellate or sessile, predominantly solitary or in 3-flowered cymules, very rarely in short axillary racemes; almost fully expanded young leaves occasionally still densely pubescent.

9 Structurally hermaphrodite flowers with the hypanthium globose-obconical ('campanulate'), indumentum sericeous; flowers distinctly pedicellate, solitary or in usually 3-flowered cymules; leaves thinly coriaceous; medium to often large canopy trees of coastal forest in Natal north of Port Shepstone, also in Swaziland, Venda, north-eastern Transvaal, extending into the FZ region . . . . . 11.3.9. *E. woodii*

9 Structurally hermaphrodite flowers with the hypanthium obconical ('infundibular'), indumentum densely villous or tomentose; flowers shortly pedicellate or sessile, solitary or very rarely in abbreviated racemes; leaves thick and coriaceous; medium sized to large canopy trees endemic to the sandstone region of southern Natal and Pondoland . . . . . 11.3.6. *E. erythrophylla*

8 Structurally hermaphrodite flowers with the hypanthium glabrous or very sparingly pubescent; flowers clearly pedicellate, solitary or rarely in short racemes; almost fully expanded young leaves essentially glabrous or only very sparingly pubescent.

10 Leaves narrowly elliptic to narrowly linear-lanceolate, (4)5–6(8) mm wide; midrib flat below in fresh material, only slightly concave above when dried; flowering mainly in June and July; densely leafed shrubs or small trees endemic to the sandstone region of southern Natal and Pondoland . . . . . 11.3.8. *E. verdoorniae*

10 Leaves variously shaped but rarely narrowly so, nearly always more than 15 mm wide; midrib raised below in fresh material, conspicuously channelled above when dried; flowering mainly from October to December.

11 Young leaves with the upper surface densely sericeous, hairs with a silvery sheen and often coral pink in colour; leaves thickly coriaceous, apex rounded (or almost so), rarely acute, base cuneate; petioles relatively thick, usually with a blackish colour; small trees only known from exposed forest margins on sandstone outcrops in the Port Shepstone district . . . . . 11.3.13. *E.* sp. B

11 Young leaves very sparingly pubescent with whitish appressed hairs or essentially glabrous; leaves thinly coriaceous, apex broadly acuminate, caudate-acute, acute, rarely broadly acute, base attenuate, cuneate or more or less rounded; petioles relatively thin, usually with a brownish-green colour.

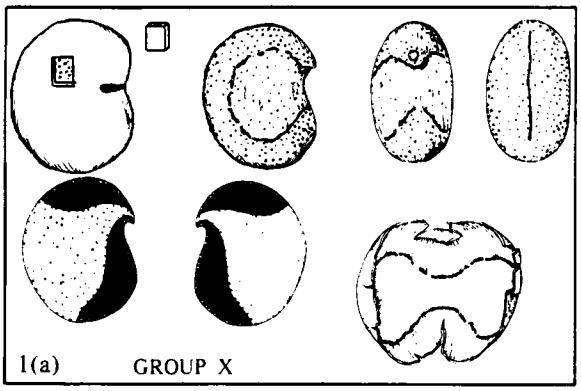
12 Leaves elliptic or obovate, apex broadly acuminate or caudate-acute, base narrowly cuneate to narrowly attenuate; large canopy trees endemic to the sandstone region of southern Natal and Pondoland . . . . . 11.3.14. *E.* sp. C

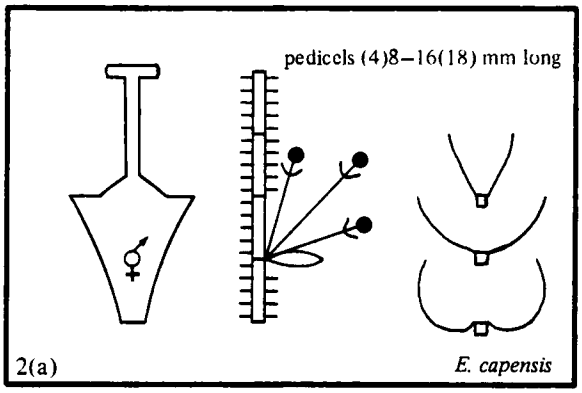
12 Leaves narrowly elliptic, elliptic-lanceolate or lanceolate, apex acute, base cuneate, broadly cuneate to more or less rounded.

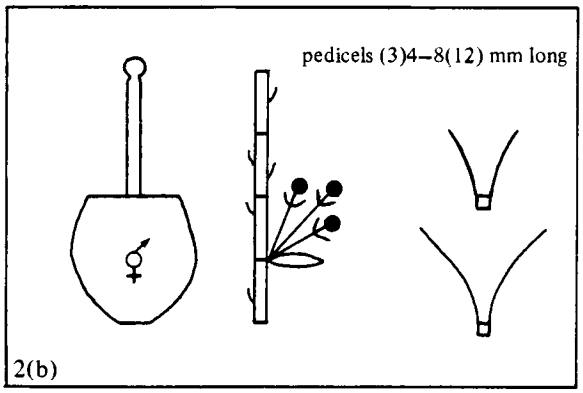
13 Leaves narrowly elliptic or occasionally elliptic-lanceolate, base cuneate or rarely broadly cuneate; midrib on the upper lamina surface of fresh leaves more or less plane and visible as a greenish line —at least towards the base of the lamina; petioles antrorse but not closely appressed to the axis; lamina only slightly ventrally deflexed at its junction with the petiole; pedicels 2–5 mm long; small to medium sized trees of relatively dry forest or shrub forest in the eastern Cape and Ciskei . . . . . 11.3.10. *E. zeyheri*

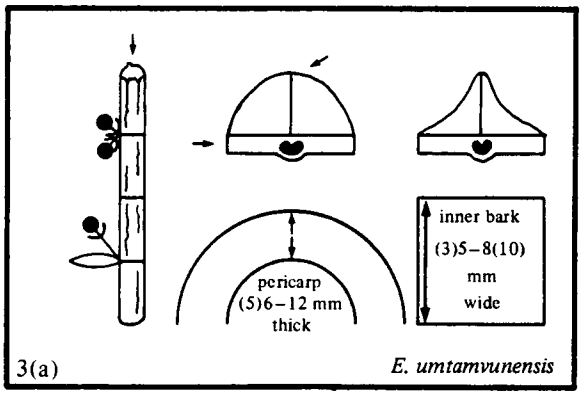
13 Leaves lanceolate, elliptic-lanceolate or occasionally elliptic; base broadly cuneate or more or less rounded; midrib on the upper lamina surface of fresh leaves completely sunken below a distinct groove formed by the adjacent lateral halves of the lamina and therefore not visible as a distinctly coloured line; petioles antrorse and more or less appressed to the axis; lamina strongly (*ca.* 80°–90°) ventrally deflexed at its junction with the petiole; pedicels (5)8–15(18) mm long; small to medium sized trees of relatively dry shrub forest, discontinuously distributed in Natal, always on sandstone . . . . . 11.3.12. *E.* sp. A

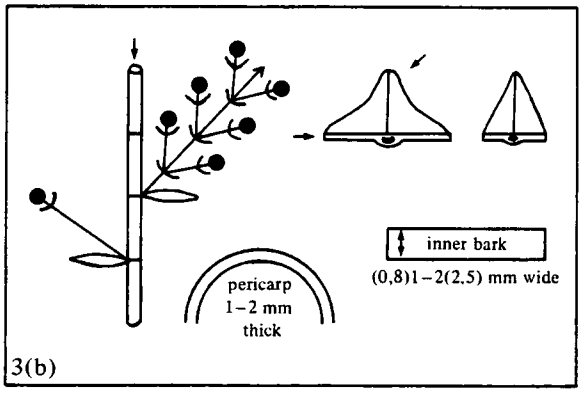
11.2.2 SIMPLIFIED PICTORIAL KEY TO THE SPECIES OF *EUGENIA*; GROUP X (COMPARE 11.2.1)

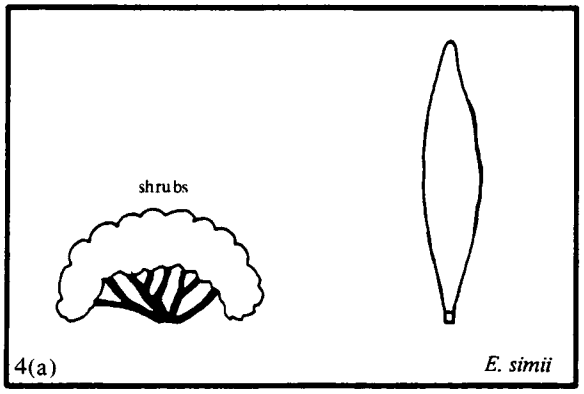


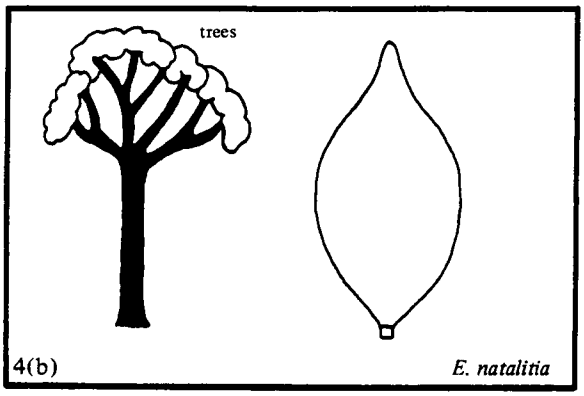




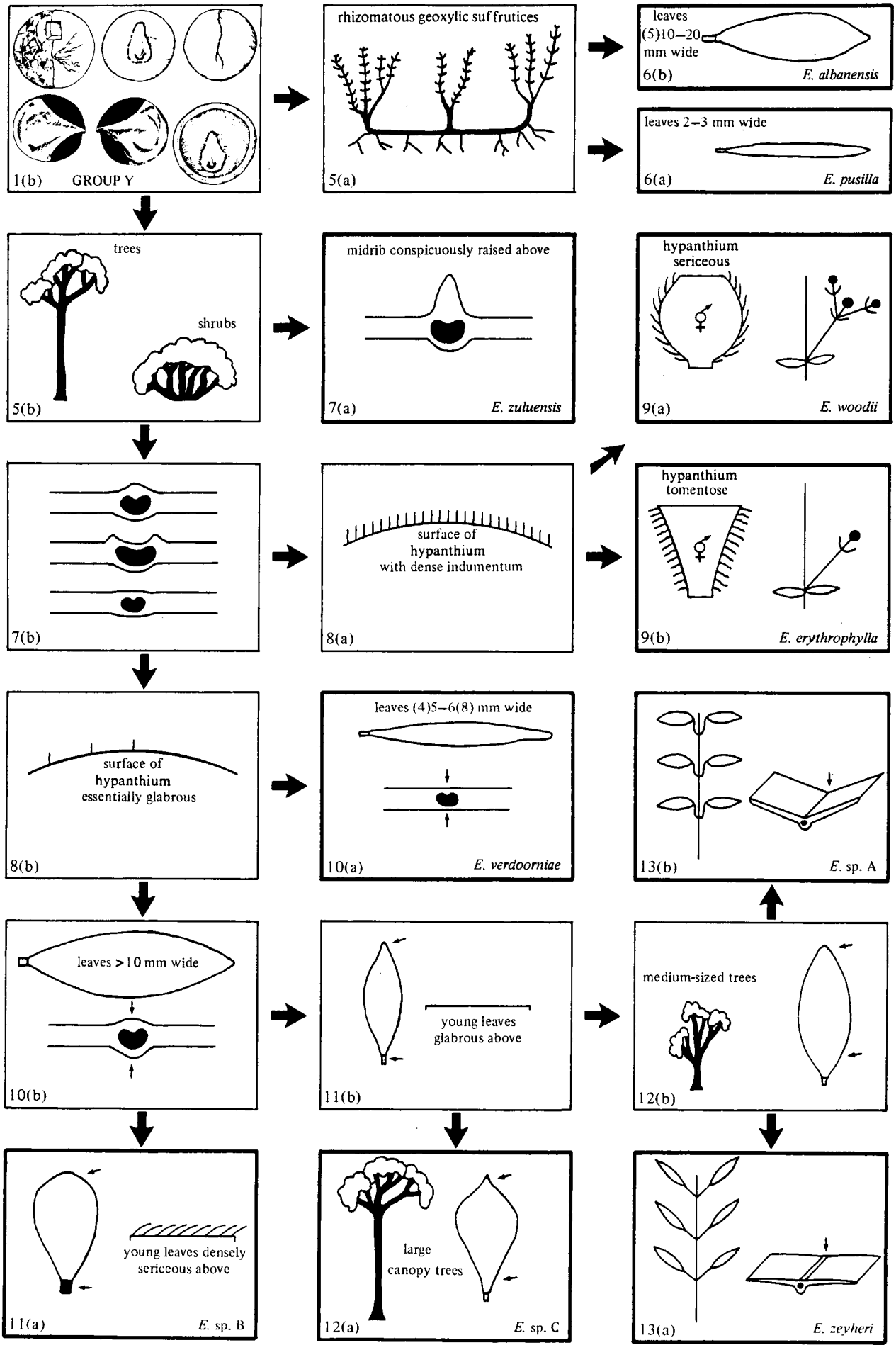








11.2.3 SIMPLIFIED PICTORIAL KEY TO THE SPECIES OF *EUGENIA*; GROUP Y (COMPARE 11.2.1)



11.3 ENUMERATION OF THE SPECIES AND SUBSPECIES

A. SPECIES GROUP X

11.3.1 ***Eugenia capensis*** (Eckl. & Zeyh.) Sond. In Harv. & Sond., FC 2: 522 (1862). Type: 'Bosjesmansrivier', *Ecklon & Zeyher* 1772 (NBG, holo.!; TCD, iso.!).

Memecylon capense Eckl. & Zeyh. in Enum. Pl. Afr. Extratrop.: 274 (1836). Type as above.

Rhizomatous suffrutices, shrubs or small trees usually on sandy soils. *E. capensis* is clearly distinct from the other species in group X. Noteworthy diagnostic features are the obconical shape of the hypanthium in structurally hermaphrodite flowers, a well developed expanded stigma, the oblong-globose shape of the seeds and the rather stiff spreading hairs on the young branchlets. It is the only native species of *Eugenia* which flowers mainly in mid-summer (January–March). Although my concept of the species is much more restricted than that of White (1977 & 1978), I also consider it a polytypic species. I recognize three subspecies in the FSA region.

Key to the subspecies of *E. capensis*

1 Shrubs or small trees up to 4 m tall; young branchlets usually with a rather dense and fairly persistent indumentum of short erect hairs; flowers with the hypanthium and petals usually sparingly gland-dotted; always on coastal dunes not far from the sea, often growing gregariously as a sand-dune binder just above the high-water level; ranging from about Port Elizabeth northward along the coast . . . . . 11.3.1.1. subsp. *capensis*

1 Rhizomatous geoxylic suffrutices usually not more than 0,5 m tall; young branchlets glabrous or with an indumentum of short erect hairs; flowers with the hypanthium and petals usually abundantly gland-dotted.

2 Leaves suborbicular or orbicular, apex broadly rounded, base subcordate to broadly rounded; young branchlets glabrous; in grassland of Transkei and particularly Natal, usually not far from the coast . . . . . 11.3.1.2. subsp. *gueinzii*

2 Leaves elliptic or elliptic-oblong, apex acute or rounded, base cuneate; young branchlets with short erect hairs or glabrous; in grassland of Maputaland ranging to the Transvaal lowveld, Soutpansberg, north-western Transvaal, probably extending to the FZ region . . . . . 11.3.1.3. subsp. A

11.3.1.1 ***E. capensis*** (Eckl. & Zeyh.) Sond. subsp. ***capensis***.

E. capensis (Eckl. & Zeyh.) Sond. var. *major* Sond. in Harv. & Sond., FC 2: 523 (1862). Type: Sandy hills between Omtendo and Omsamculo, *Drege* s.n. (not yet located).

Myrtus capensis Harv. in Gen. S. Afr. Pl.: 99 (1938) non *Eugenia capensis* (Eckl. & Zeyh.) Sond. Type: sand-hills between the Zwartkops and Koega Rivers, ? *Zeyher* 2466 (not yet located).

Subspecies *capensis* is essentially a plant of coastal sand-dune thicket. It is easily distinguished by the more or less orbicular leaves which are thick and coriaceous as well as the almost eglandular petals. Var. *major* was originally distinguished mainly by its larger leaves. However, leaf size gradually decreases from north to south along the coast and there is no point in maintaining this subspecies. Plants of subspecies *capensis* bordering on grassland and destroyed by fire resemble subsp. *gueinzii* when new growth resumes.

FIGURE 1, page 214.

REPRESENTATIVE SPECIMENS: *Botha & Van Wyk* 985, 986, 987, 1002; *Van Wyk* 2345, 2586, 2587, 2588, 2589, 2618, 2643, 3166, 3218, 3227, 3245, 3348, 4509 (all in PRU).

11.3.1.2 ***E. capensis*** (Eckl. & Zeyh.) Sond. subsp. ***gueinzii*** (Sond.) F. White in Kirkia 10: 403 (1977). Type: Port Natal, *Gueinzius* s.n. (TCD, holo.!; K, iso.!).

E. gueinzii Sond. in Harv. & Sond., FC 2: 523 (1862). Type as above.

Subsp. *gueinzii* is a grassland suffrutex, obviously closely related to subsp. *capensis* and adapted to frequent burning. It is distinguished by the rhizomatous habit, glabrous young shoots and conspicuously gland-dotted petals. Leafy shoots are practically indistinguishable from those of subspecies *capensis* because the latter subspecies occasionally produces glabrous shoots. Subsp. *gueinzii* occurs in relatively moist grassland in the coastal belt of Transkei and Natal. Good examples can be found at Fair Acres Estate near Oribi Gorge. In my 1978 thesis *E. gueinzii* was not maintained as a distinct taxon, but relegated to the synonymy of *E. capensis*. Subsequently I have decided to follow White in recognizing it at the subspecific level.

FIGURE 2, page 215.

REPRESENTATIVE SPECIMENS: *Van Wyk* 2340, 5120, 5413, 6686, 6690; *Van Wyk & Venter* 1299, 1308 (all in PRU); *Wood* 12426 (PRE).

11.3.1.3 ***E. capensis*** (Eckl. & Zeyh.) Sond. subsp. **A.** This subspecies probably falls within the concept of *E. capensis* (Eckl. & Zeyh.) Sond. subsp. *aschersoniana* (F. Hoffm.) F. White in Kirkia 10: 403 (1977). Type from Tanzania and not yet studied.

Up to now I have referred to this taxon as *E.* cf. *mossambicensis*. I adopted the latter name on the authority of the late Mme G.J.M. Amshoff of Wageningen who determined sheets of this taxon now in PRE, as *E. mossambicensis* Engl. Unfortunately I have not seen the type of this species, viz. *Schlechter* s.n. (B†, holo.; BM, drawing). White (1978) maintained that *E. mossambicensis* constitutes specimens intermediate between subspp. *capensis* and *aschersoniana*. This may well be the case, but I am reluctant to draw final conclusions at this stage because I have not yet studied the relevant type material.

Subsp. A is distinguished mainly by its more or less elliptic leaf blades that are more tapering towards both ends than in subspp. *capensis* and *gueinzii*. The young

shoots are frequently hairy thereby recalling subsp. *capensis*. Over the greater part of its range it can easily be separated from the other two subspecies. However, in the coastal areas of Maputaland subsp. A seems to intergrade with subspp. *capensis* and *gueinzii*.

Indications are that subsp. A ranges north into the FZ region. Its affinities with taxa such as *E. malangensis* (O. Hoffm.) Niedenzu, *E. angolensis* Engl., *E. marquesii* Engl., *E. poggei* Engl., *E. laurentii* Engl. and *E. stolzii* Engl. & Von Brehm. need further study.

FIGURE 3, page 216.

REPRESENTATIVE SPECIMENS: *Botha & Van Wyk* 990, 992, 1149 (PRU); *Kruger* 341 (PRE); *Van Wyk* 2494, 2495, 2550, 5940, 5951(b), 6679 (PRU).

11.3.2 ***Eugenia natalitia*** Sond. in Harv. & Sond., FC 2: 522 (1862). Syntypes: Port Natal, *Gueinzius* 60 & 568 (not yet traced); near D'Urban, *Garrard & McKen* 707 (TCD, syn.!).

E. capensis (Eckl. & Zeyh.) Sond. subsp. *natalitia* (Sond.) F. White in Kirkia 10: 402 (1977), pro parte. Type as above.

?E. natalitia Sond. var. *medleyiana* Engl. & Von Brehm. in Bot. Jb. 54: 329 (1917). Type: Durban, *Wood* 9288 (not yet traced).

E. rudatisii Engl. & Von Brehm. in Bot. Jb. 54: 335–336 (1917). Type: Natal, Fairfield, Illutemkunga, *Rudatis* 1547 (B†, holo.; K, iso.!).

E. natalitia is a variable species with both tree and shrub (rare) forms. It differs from *E. capensis* by the globose-obconical hypanthium in structurally hermaphrodite flowers, a slightly capitate or punctiform stigma, glabrous or very sparingly appressed pubescent young shoots and various other distinctions (see key). Similar to *E. capensis*, it consists of various forms which are, however, more difficult to demarcate for the purpose of recognizing infraspecific taxa. Noteworthy variations are an often shrubby form in northern Natal (particularly common at Ngoye) with light green leaves and a weakly crenate leaf margin. Also in northern Natal is a form with relatively long, narrow leaves in the Empangeni–Richards Bay area and a form with the leaf apex prominently caudate-acuminate in the forests of the Hluhluwe Game Reserve. A riverine form with narrowly elliptic leaves occurs along the Blyde River and its tributaries in the north-eastern Transvaal.

Both *E. simii* and *E. umtamvunensis* appear to be derived from *E. natalitia*. Alternatively, the former two species could perhaps be treated as subspecies of *E. natalitia*. There are indications that *E. natalitia* resembles *E. capensis* in being a polytypic species, with many variants in various parts of Africa. I do not, however, consider *E. natalitia* closely related to *E. capensis*. The treatment of the former taxon as a subspecies of the latter (as suggested by White), is therefore unacceptable. Owing to parallel trends in leaf shape, *E. natalitia* may easily be confused with *E. simii, E. woodii, E. zuluensis, E. umtamvunensis* and *E.* sp. C.

FIGURE 4, page 217.

REPRESENTATIVE SPECIMENS: *Abbott* 1515; *Lowrey & Van Wyk* 1044; *Van Wyk* 2539, 2574, 2583, 2699, 2793, 3289, 3856, 4078, 5153, 5373, 5388, 5417, 6024; *Van Wyk & Kok* 5869; *Van Wyk & Theron* 4532, 4725, 4820 (all in PRU).

11.3.3 ***Eugenia simii*** Duemmer in Gdnrs' Chron. ser. 3, 52: 179, t. 83 (1912). Type: Natal, Zululand, *Gerrard* 47 (K, holo.!; BM, iso.).

E. capensis (Eckl. & Zeyh.) Sond. subsp. *simii* (Duemmer) F. White. Type as above.

E. simii is a riverine shrub closely related to *E. natalitia*. It occurs, often in abundance, along watercourses between the Umzimkulu and Umtamvuna Rivers in southern Natal. Hundreds of plants can be seen near the bridge over the Umzimkulwana River in the Oribi Gorge Nature Reserve. In the field, *E. simii* can easily be separated from *E. natalitia* by its densely leaved, shrubby growth form and narrowly elliptic leaves. Although *E. simii* and *E. natalitia* may recall two ecotypes, they occasionally occur in the same habitat. 'Typical' *E. natalitia* grows for example on the banks of the Izotsha river just upstream from the Izotsha Waterfall and in close proximity to *E. simii*. The fact that the two species do occur together substantiates their treatment as separate taxa.

There is an interesting distinction between *E. simii* and *E. natalitia* which one is unable to obtain from herbarium specimens. In cultivation plants of *E. simii* develop a very robust and thick stem and root system compared to that of *E. natalitia*. This is probably an adaptation to the riverine habitat of the species and may explain why in nature plants are not uprooted and washed away during floods. In fact, plants of *E. simii* are frequently subjected to floods and considering the rocky streambeds where they grow, plants must periodically be exposed to considerable abrasive forces.

E. simii can be confused with narrow leaved variants of *E. natalitia* from other parts of the FSA region. Such forms from the lower reaches of the Tugela River in northern Natal and from the Blyde River and its tributaries in the north-eastern Transvaal, probably constitute independent developments now resembling the plants from southern Natal. Specific status is given to the southern Natal plants because there are large populations in nature and they are confined to a well defined geographical area, viz. the sandstone 'edaphic island' of southern Natal and Pondoland. In addition, variation between *E. simii* and *E. natalitia* is essentially discontinuous in the latter region. An alternative approach would be to treat *E. simii* as a subspecies of *E. natalitia*. I do not have any serious objections against such a step, which I believe, would be very much a subjective decision.

There is a real possibility that the name, *E. simii*, is not applied in its correct sense. The type specimen of *E. simii* has slightly larger leaves and longer internodes

than the frequently encountered state in the southern Natal plants. Could the type specimen then not perhaps be from one of the narrow leaf variants of *E. natalitia* in northern Natal, particularly from forms between the Tugela River and Richards Bay? The locality on the type specimen is vague, but 'Zululand' indeed strengthens the suspicion that it was not collected in southern Natal. On the other hand, plants from the latter region, and growing in shady positions, do match the type collection. At the moment, the only way to try and clear up these uncertainties is to study the collecting track of Gerrard in Natal. Provisionally, I therefore apply the name *E. simii* to the southern Natal plants with the full realization that it might be incorrect.

In the protologue Duemmer compared *E. simii* with *E. zeyheri*. Indeed, the two species may be confused because of their narrow, more or less elliptic leaves. *E. zeyheri*, however, belongs to species group Y and is not at all closely related to *E. simii*.

FIGURE 5, page 218.

REPRESENTATIVE SPECIMENS: *Van Wyk* 2336, 2609, 3274, 3296, 4172, 4173, 4175, 4176, 4177, 4243, 6029; *Van Wyk & Venter* 1273, 1304, 1334 (all in PRU).

11.3.4 ***Eugenia umtamvunensis*** Van Wyk in S. Afr. J. Bot. 1(4): 158–162. Type: Natal, 3030 (Port Shepstone): Beacon Hill near Port Edward (–CC), *Van Wyk* 3631 (PRU, holo.!; NH, PRE, iso.!).

For a description of the species and a discussion of its affinities see Van Wyk (1982), page 189 . The following notes supplement the article.

Since the description of *E. umtamvunensis*, many more plants of the species were discovered in the Umtamvuna Nature Reserve (UNR) and recently also further south along the Mtentu River in Pondoland. The species appears to be much more variable than intially believed. Particularly leaf size and shape vary considerably. Forms of *E. umtamvunensis* from exposed plateaus in the UNR have a shrubby growth form and rather narrow leaves, strongly reminiscent of *E. simii*. To add to the confusion, the leaf apex is occasionally more or less acute thereby recalling *E. natalitia*. Features which appear to be fairly reliable are the thick and stout young shoots, covered by a rusty reddish-brown bark. The mature bole bark is exceptionally thick, but unfortunately this feature is only reliable for diagnostic purposes in tree forms. One additional record of fruiting material confirmed the presence of a relatively thick pericarp. These fruits were, however, 1-seeded, and indicated that 2-seeded fruits are not a constant feature of the species as suggested in Van Wyk (1982). It nevertheless shows that the very thick pericarp in the 2-seeded fruits is not entirely due to the presence of more than one seed, but that it is an inherent feature of the species.

E. umtumvunensis is very closely related to *E. natalitia* and could alternatively be treated as a subspecies of the latter. On a few rare occasions isolated trees which seemed to be intermediate between these two species were found. Separate specific status nevertheless seemed to be warranted when plants of both species growing sympatrically at the same site are encountered in nature, for example in the UNR at the 'Amphitheatre' forest.

FIGURE 1 & 3, page 190 & 192 and FIGURE 6, page 219.

REPRESENTATIVE SPECIMENS: *Abbott* 1305, 1611, 2556; *Van Wyk* 3283, 3338, 3341, 4210, 4230, 4232, 4234, 5030, 5132, 5134, 5374, 5379, 5385, 5395, 5400, 6093, 6136 (all in PRU).

A new species of *Eugenia* (Myrtaceae) from southern Natal

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Eugenia umtamvunensis Van Wyk, a new species from southern Natal is described. It is closely allied to *E. natalitia* Sond. Differentiating characteristics include the more leathery foliage leaves with obtuse or rounded apices, conspicuous flowering brachyblasts on branchlets of previous seasons, flowers sessile or with relatively short pedicels and larger, two-seeded fruits with a much thicker pericarp.

S. Afr. J. Bot. 1982, 1: 158 – 162

Eugenia umtamvunensis Van Wyk, 'n nuwe spesie van Suid-Natal word beskryf. Dit is nou verwant aan *E. natalitia* Sond. Onderskeidende kenmerke sluit in die meer leeragtige blaarlaminas met stomp of geronde punte, opvallende blomdraende bragiblaste op die takke van vorige seisoene, sittende blomme of met relatief kort blomstele en groter, twee-sadige vrugte met 'n veel dikker perikarp.

S.-Afr. Tydskr. Plantk. 1982, 1: 158 – 162

Keywords: *Eugenia*, Myrtaceae.

Introduction

A number of undescribed species presently included in the genus *Eugenia* L. s.str. occur in southern Africa. Two species groups (X and Y) are distinguished among the native members of the genus (Van Wyk 1978; additional papers cited under discussion). One of these new species belongs to Group X and is described in this paper. The exact taxonomic position of Group Y is doubtful and its new taxa must await formal description pending further study.

Description

Eugenia umtamvunensis Van Wyk, **sp. nov.**, *E. natalitia* affinis, a qua imprimis differt ramulis crassioribus et rigidioribus, cortice primo atro-ferruginea, foliis magis coriaceis, apicibus obtusioribus vel rotundatis, brachyblastis floriferis in ramulis vetustioribus plures annos florentibus, floribus vel sessilibus vel cum pedicellis relative brevioribus, fructibus maioribus ac globosioribus et saepe sessilibus et plerumque biseminalibus et cum crassiore pericarpio.

Type. — Natal, 3030 (Port Shepstone): Beacon Hill near Port Edward (– CC), *Van Wyk* 3631 (PRU, holo.; NH; PRE).

Androdioecious tree up to 10 m high. *Bark* grey or whitish, smooth or flaking off in thick irregular pieces, slash dark brown. *Branchlets* dark rusty-brown becoming grey when mature, often with irregular longitudinal ribs, initially flattened, glabrous; buds glabrous to densely pubescent; internodes (7)15 – 25(35) mm long. *Leaves* decussate, petiolate, lamina reddish-brown when young, becoming deep green and shiny above, light green, dull and clearly dotted with secretory cavities below, glabrous, usually elliptic to broadly elliptic or obovate to broadly obovate, (25)40 – 80(90) mm long, (15)30 – 55(60) mm wide; apex obtuse or rounded and sometimes shortly and bluntly acuminate; base obtuse, thick and coriaceous; margin revolute in dried and fresh leaves; venation pinnately net veined, midrib in dried leaves usually with basal half concave and slightly raised, or plane in upper half above, strongly elevated below; plane or slightly elevated above and prominently elevated below in fresh leaves; primary lateral veins alternate or opposite, (3)5 – 6(8) pairs, spreading, raised on both sides in dried

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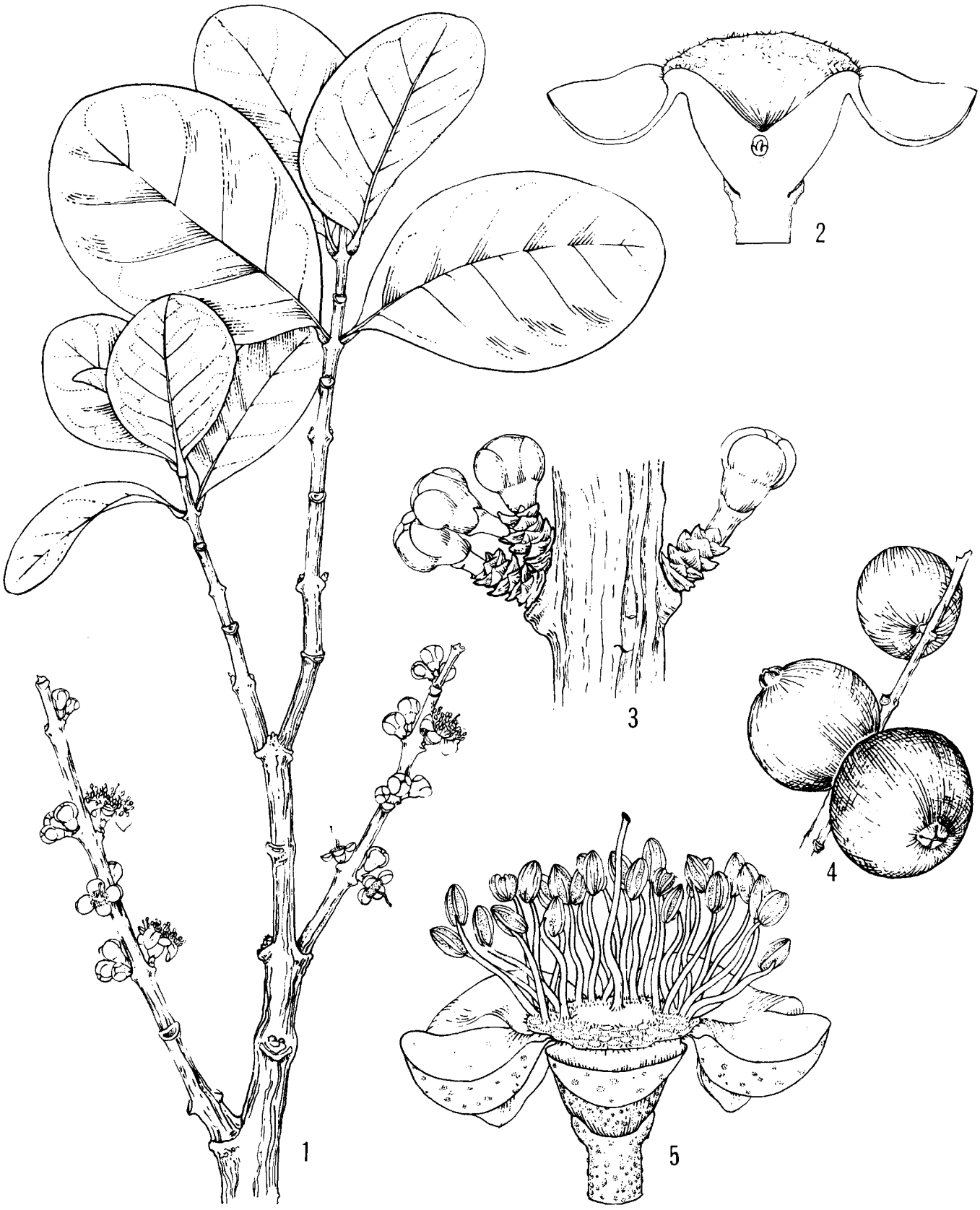

Figure 1 *Eugenia umtamvunensis*. 1, leafy twig with flowers, × 1 (*Van Wyk* 5132); 2, longitudinal section of staminate flower with petals and stamens removed, × 8 (*Van Wyk* 5132); 3, brachyblasts with flower buds, × 4 (*Van Wyk* 4210); 4, branchlet with fruits, × 1 (*Van Wyk* 3631); 5, bisexual flower with some petals and stamens removed, × 8 (*Van Wyk* 5134).

leaves, slightly raised or flat on both sides in fresh leaves, fused into a longitudinal lobed marginal vein about 1 – 4(6) mm from the margin of the lamina; tertiary veins slightly raised on both sides in dried leaves, obscure in fresh ones; petiole (2)3 – 4(5) mm long, ventrally plane, glabrous. *Inflorescences* consisting of usually 1 – 5 brachyblasts (fasciculiform-racemiform conflorescences) up to 6 mm long in the axils of fallen leaves on branchlets of previous

seasons, each brachyblast with 1 – 5 flowers and remaining floriferous for a number of seasons, very rarely with flowers solitary in the axils of bracts on the first few nodes of the new season's growth. *Staminate flowers* sessile or with pedicels up to 4(6) mm long; bracteoles 2, fleshy, attached at the base of the hypanthium, *ca.* 1,0 mm long, *ca.* 0,75 mm wide, ovate with the apex obtuse or rounded, glabrous or with a few scattered hairs, secretory cavities usually present. *Sepals* 4, subrotund with rounded apices, 2 large, *ca.* 3,0 mm long, *ca.* 3,2 mm wide, 2 small, *ca.* 2,0 mm long, *ca.* 3,0 mm wide, outer surface sparingly gland-dotted, glabrous or margins often with a few scattered hairs. *Petals* 4, white, usually elliptic or ovate, *ca.* 5,0 mm long, *ca.* 4,0 mm wide, glabrous or with a few scattered hairs on the margin, sparingly gland-dotted. *Disc* with a central depression, surface even, fleshy and sparingly pubescent between filaments. *Stamens* usually 40 – 55, arising from the disc in *ca.* 3 series; filaments of various lengths, *ca.* 2 – 6 mm long; anthers 2-thecous, 1 × 0,75 mm, all fertile. *Hypanthium* more or less obconical, *ca.* 1,75 mm long, glabrous and conspicuously gland-dotted. *Ovary* aborted or rudimentary; style rudimentary, *ca.* 0,5 mm long or absent. *Bisexual flowers* with the pedicels, bracteoles, *sepals, petals* and *stamens* as in staminate flowers. *Disc* slightly convex with an even surface, fleshy, sparingly pubescent between filaments, with a smooth zone *ca.* 1,0 mm wide surrounding the base of the style. *Hypanthium* obconical, *ca.* 2,0 mm long, resembling that of the staminate flowers. *Ovary* fused to the lower part of the hypanthium, 2-locular; ovules usually 2 per locule, 2 or rarely 1 or 3 developing; style filiform, terete, glabrous, *ca.* 4,5 mm long; stigma small, somewhat capitate, covered with small papillae. *Fruit* a fleshy berry, changing yellow through reddish-orange to dark purple when ripe, subglobose, usually 25,0 – 30,0 mm diam., glabrescent with persistent calyx lobes at the apex; pericarp 6,0 – 12,0 mm thick, flesh whitish. *Seeds* subreniform to oblong globose, often with one flattened lateral side in 2-seeded fruits, testa leathery, *ca.* 0,25 mm thick, brownish; embryo with cotyledons partly fused, gland-dotted (Figure 1).

Flowers were collected during October/November and ripe fruits in February.

Distribution

The first collections of *E. umtamvunensis* were made on the farm Beacon Hill near Port Edward in 1979. In January 1982 a further number of trees of this species were discovered a few kilometres to the south of Beacon Hill in the adjoining Umtamvuna Nature Reserve. Known only from these two localities, *E. umtamvunensis* not only shows the most restricted distribution of the native tree species of *Eugenia*, but is one of the rarest trees in southern Africa (Figure 2).

E. umtamvunensis is a forest tree growing on sandy, poor black acidic soil overlaying Table Mountain sandstone. It has been found growing in association with *E. erythrophylla* Strey, *E. verdoorniae* Van Wyk, an undescribed *Eugenia* species (all belonging to Group Y) and *E. natalitia* Sond. (Group X). Other associated trees often include rare species such as *Beilschmiedia natalensis* J.H. Ross, *Manilkara nicholsonii* Van Wyk, *Memecylon grandiflorum* R. & A. Fernandes, *Pseudoscolopia polyantha* Gilg and *Rhynchocalyx lawsonioides* Oliv.

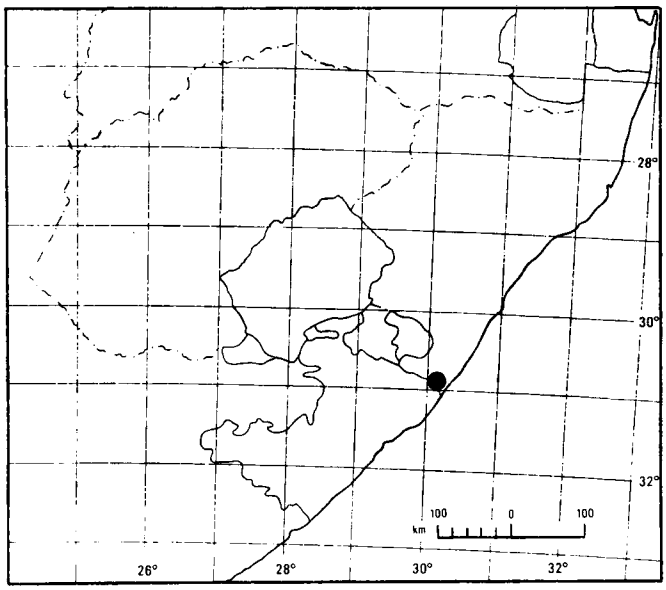

Figure 2 Distribution of *Eugenia umtamvunensis*.

Specimens examined

NATAL.—3030 (Port Shepstone): Beacon Hill near Port Edward (– CC), *Van Wyk 3283, 3338, 3341, 3631* (PRU, holo.; NH; PRE), *4210, 4230, 4232, 4502, 5030, 5132, 5133, 5134, 5135* (all in PRU); Umtamvuna Nature Reserve, Amphitheatre, *Van Wyk 5374, 5379, 5385, 5395, 5400* (all in PRU).

Discussion

Judged by the criteria established for the morphology of the first-formed stem periderm (Van Wyk *et al.* 1980), seeds (Van Wyk 1980) and stomata (Van Wyk *et al.* 1982), *E. umtamvunensis* without doubt belongs to Group X. It is evidently closely allied to the widespread *E. natalitia*. Although both species occur sympatrically in the Umtamvuna Nature Reserve, no intermediate plants have been found during field work.

E. umtamvunensis differs from *E. natalitia* in especially the thicker and stouter branchlets, initially covered by a darker rusty-brown bark; more leathery leaves; blunter or rounded leaf apices; brachyblasts on the older branchlets that remain floriferous for more seasons; flowers sessile or with relatively short pedicels; larger, more globose and often sessile fruits which are predominantly 2-seeded and with a much thicker pericarp.

Sessile flowers are absent in *E. natalitia* where the pedicels are usually (3)4 – 8(12) mm long. The short axillary racemes (anauxotelic inflorescences according to Briggs & Johnson 1979) frequently found in this species, appear to be absent in *E. umtamvunensis*. Brachyblasts, when present in *E. natalitia*, are never conspicuous and remain floriferous for a limited number of seasons (probably two or three).

Fruits of *E. umtamvunensis* are edible with a sweetish, although somewhat acrid, taste. Maximum thickness of the pericarp varies from 1,0 – 2,0 mm in *E. natalitia* and from 6,0 – 12,0 mm in *E. umtamvunensis*. Of all the species included in Group X, *E. umtamvunensis* possesses by far the largest fruit and thickest pericarp. The fruits of *E. um-*

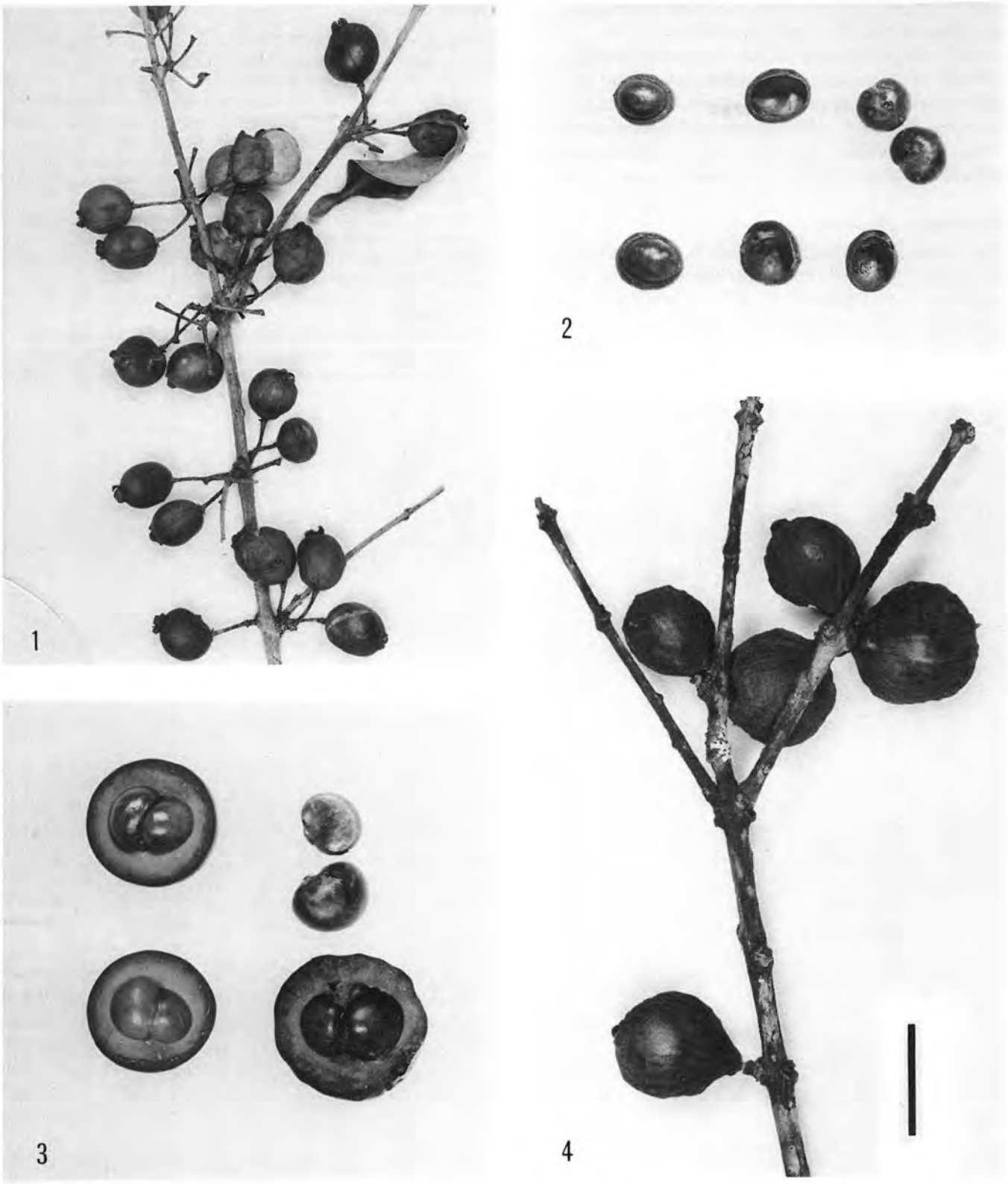

Figure 3 Fruits of *Eugenia natalitia* (1 & 2) and *E. umtamvunensis* (3 & 4). Almost ripe fruits from herbarium specimens: 1, *E. natalitia* (*Hemm* s.n.); 4, *E. umtamvunensis* (*Van Wyk* 3631). Cut-open FAA-preserved ripe fruits with intact and removed seeds: 2, *E. natalitia* (*Van Wyk* A138); 3, *E. umtamvunensis* (*Van Wyk* 3631). All natural size (length of scale = 20 mm).

tamvunensis are predominantly two-seeded. This is unique among species of both groups which are usually one- and only rarely up to three-seeded. However, more fruiting material is required to ascertain the constancy of this feature (Figure 3).

Owing to its robust habit and thick leathery leaves, *E. umtamvunensis* is more likely to be confused with *E. erythrophylla* than with *E. natalitia*. However, in *E. erythrophylla* the young leaves are densely tomentose and the abaxial lamina surface of mature leaves is usually whitish-green with the secretory cavities obscure. Young leaves of *E. umtamvunensis* are glabrous and the abaxial

surface of the mature lamina is usually light green with the secretory cavities clearly visible.

With the description of *E. umtamvunensis*, another tree is added to the growing list of species endemic to the Table Mountain sandstone area of southern Natal and northern Transkei (Van Wyk 1981). This unique centre of endemism offers considerable scope for further study especially by students of plant geography, systematics and ecology.

Acknowledgements

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B. SPECIES GROUP Y

11.3.5 ***Eugenia albanensis*** Sond. in Harv. & Sond., FC 2: 522 (1862). Syntypes: Hills on the Great Vishriver, *Zeyher, Memecyl* 1 (TCD, syn.!; PRE, isosyn.!); between Kowie and Kapriver, *Drege* 5366b (not yet traced); near Somerset, *Bowker* s.n. (TCD, syn!; K, isosyn.!).

E. capensis (Eckl. & Zeyh.) Sond. subsp. ***albanensis*** (Sond.) F. White in Kirkia 10: 402 (1977). Type as above.

E. albanensis is a well defined species closely related to *E. pusilla* (see 11.3.7). These two species are the only members of species group Y which are rhizomatous geoxylic suffrutices. *E. albanensis* is, in my opinion, always a suffrutex, usually not more than 0,4 m high. Plants form extensive clones in grassland, particularly in the coastal regions of the eastern Cape, Ciskei, Transkei and Natal. Isolated populations were recently discovered in the eastern Transvaal near White River and Nelspruit. White (1978) claimed that *E. albanensis* occurs as a shrub or small tree (up to 8 m tall) in the extreme south of Mozambique and in adjacent parts of Maputaland (= Tongaland). This claim needs further investigation, although I am almost sure that the shrubs and trees referred to by White represent *E. woodii* susbp. *woodii*. Confusion between the two species is possible owing to similarities in leaf shape and the presence of 3-flowered cymules in both these taxa. Leaf shape in *E. albanensis* is rather variable but in the coastal areas north of St. Lucia (including Maputaland) the leaves may be distinctly spathulate. Leaves from the latter plants are very similar to the obovate, or more rarely, spathulate leaves in *E. woodii* subsp. *woodii* which occurs in forest patches in the same area. *E. albanensis* and *E. woodii* are the only native species of *Eugenia* with 3-flowered cymules. However, cymules are not very common in *E. albanensis* and are absent in some plants. Despite these similarities, *E. woodii* subsp. *woodii* are shrubs or trees whereas *E. albanensis* is a small suffrutex. Another noteworthy feature of *E. albanensis* is the often leaf-like bracteoles in some flowers, particularly in plants actively sprouting and flowering after burning. *E. albanensis* has the smallest growth form within species group Y but, strangely, the largest fruits. Fruits up to 50 mm diameter were recorded. These are known as 'vlakappels' or Myrtle apples. They are edible with a unique refreshing taste, making the fruits of this species the most palatable of the native eugenias (Van Wyk 1985; page 195).

E. albanensis is sometimes confused with *E. capensis* subsp. A with which it shares the same growth form. Besides the fact that the two taxa belong to different groups of species, the more discolourous leaves of *E. albanensis* may be used in the field to distinguish it from the latter taxon. Confusion with *E. zeyheri* is also possible, especially if the habit of the plants is unknown and only sterile material is available for identification. Occasionally the characteristic shape of slightly wilted leaves in *E. albanensis* may aid in its recognition. Such leaves have the lamina margin conspicuously revolute and the apex curved upward.

FIGURE 7, page 220.

REPRESENTATIVE SPECIMENS: *Kluge* 1422; *Van Wyk* 2581, 3171, 3176, 3209, 3217, 3249, 3276, 3278, 5265; *Van Wyk & Kok* 5811; *Van Wyk & Lowrey* 6814; *Van Wyk & Venter* 1264 (all in PRU).

DIE VLAKAPPEL—'n VERGETE VELDVRUG

deur A. E. van Wyk
(H. G. W. J. Schweickerdt-herbarium, Departement Plantkunde, Universiteit van Pretoria)

INHEEMSE PLANTE MET eetbare vrugte is gewoonlik wyd bekend en het by natuurliefhebbers geen bekendstelling nodig nie. Dit is daarom verbasend dat een van ons opvallendste en smaaklikste veldvrugte, die vlakappel, vandag oënskynlik vry onbekend is — veral in dele van Natal waar die spesie baie volop is.

Die vlakappel was vroeër bekend en gewild onder koloniste in veral die Oos-Kaap en word selfs vandag nog as 'n lekkerny deur sommige swart volke beskou. Tog kan daar geen verwysing na die spesie in bekende bronne oor inheemse veldkosse gevind word nie. Hierdie artikel het ten doel om die status van die vlakappel as 'n uitstekende eetbare veldvrug in ere te herstel en te bespiegel waarom dit in vergetelheid verval het. Inligting oor verskeie wetenswaardighede, waaronder aspekte rakende geografiese verspreiding, klassifikasie, volksname, morfologie en kweking word ook verskaf.

1: Donkergroen plate vlakappelplante vertoon opvallend in kort-geweide grasveld (Piggot Park, Grahamstad). 2: Sappige vlakappels wat die mond laat water. Muntstuk 30 mm in deursnee. Versamel in grasveld by Port Edward. 3 en 4: Vlakappelplante met omringende grasverwyder om die opvallende ryp vrugte wat naby grondvlak gedra word, te toon. Let op die kleurvariasie.

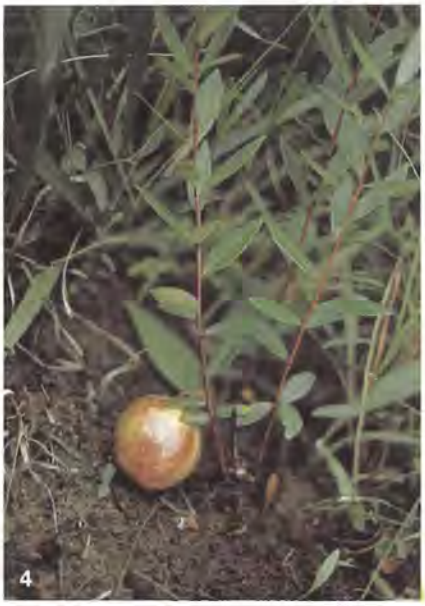
Klassifikasie

Die wetenskaplike naam vir die vlakappel is *Eugenia albanensis* en dit behoort aan die familie Myrtaceae (bloekom-familie). Dit is in 1862 deur O. W. Sonder in die Flora Capensis beskryf op grond van materiaal wat in die Oos-Kaap (Albanië-distrik) versamel is.

Eugenia is een van die grootste houtagtige genusse in die wêreld en die meerderheid van die bykans 1 000 spesies word in tropiese woude van Suid-Amerika aangetref. *Eugenia* word geklassifiseer onder die subfamilie Myrtoideae wat onder andere deur die aanwesigheid van vlesige vrugte gekenmerk word. Die koejawel (*Psidium guajava*) wat op groot skaal vir sy vrugte aangeplant word, is seker die bekendste verteenwoordiger van hierdie subfamilie. Min *Eugenia*-spesies word egter kommersieel vir hul vrugte verbou. *E. uniflora* ("pitanga" of "Surinam cherry") met eetbare, helder oranje-rooi geribde vrugte word dikwels, veral in Natal, in tuine opgemerk. Dit is selfs al op plekke langs die Natalse kus genaturaliseer. Die sogenaamde "*E. australis*" wat orals in tuine aangeplant word, is eintlik nie 'n *Eugenia*-spesie nie, maar *Syzygium paniculata*, afkomstig uit Australië en naverwant aan ons inheemse waterbessies.

In Suider-Afrika is die grootste konsentrasie *Eugenia*-spesies in Natal waar ongeveer 13 (sommige nog onbeskryf) aangetref word. Al die inheemse spesies het eetbare vrugte waarvan smaaklikheid van spesie tot spesie verskil. Spesies wat naverwant is aan *E. albanensis* sluit in *E. erythrophylla*, *E. verdoorniae*, *E. woodii*, *E. zeyheri* en *E. zuluensis*.

White (1977, 1978) klassifiseer die vlakappel as 'n subspesie van die blouduinebessie (*E. capensis* subsp. *capensis*) en stel die nuwe



kombinasie *E. capensis* subsp. *albanensis* voor. Daar is egter aanduidings dat die twee spesies geensins naverwant is nie en daarom word die voorgestelde klassifikasie nie hier nagevolg nie.

Volksname

Een van die nadele van volksname is dat die dieselfde spesie onder meer as een naam bekend kan wees. Dit is moontlik ook met *E. albanensis* die geval. Die naam "vlakappel" is afkomstig uit die Oos-Kaap waar dit vandag nog gebruik word (soms verkeerdelik toegeskryf aan *E. zeyheri*). "Wilde-appelkoos" en "wilde-appel" wat in 1813 deur William Burchell in die omgewing van Port Alfred aangeteken is, verwys waarskynlik ook na *E. albanensis* (cf. Burchell nrs. 3948, 4061 & 4152). Van der Merwe *et al.* (1967) noem die spesie "wilde-aarbei", hul eie skepping wat op die smaakooreenkoms met die aarbei dui.

"Vlakappel" is 'n baie beskrywende naam omdat dit na die oop, grasveldhabitat van die plant verwys ("vlakte" soos in byvoorbeeld "vlakvark" en "vlakhaas") asook die vorm van die vrugte wat aan dié van 'n appel herinner. In Engels is die oudste naam wat ek kon opspoor "myrtle apples", verwysende na die ooreenkoms wat die vrugte met dié van die gewone Europese mirt (*Myrtus communis* — 'n verlangse familielid) vertoon.

In Natal is die naam "Unobebe" (Zoeloe), "u-Nanja", "iNjanji" en "Nanjwa" (Zoeloe/Tonga) aangeteken. Laasgenoemde drie is blykbaar variasies van dieselfde naam.

Geografiese verspreiding

Die hoof-verspreidingsgebied van die vlakappel is in Natal waar dit lokaal volop is in grasveld langs die kus en soms ook in die dele van die middelland (byvoorbeeld Nkandla en die omgewing van Pietermaritzburg). Hiervandaan strek die verspreiding in 'n strook min of meer parallel met die kus noordwaarts tot in die suide van Mosambiek en suidwaarts deur Transkei en Ciskei tot in die omgewing van Grahamstad.

Tot onlangs is aanvaar dat die vlakappel tot bogenoemde gebied beperk is. Dit was daarom 'n verrassing toe die kurator van die Laeveldse Botaniese Tuin, mnr. Johan Kluge, 'n geïsoleerde bevolking gedurende 1977 op die Witklipstaatsbos, tussen Witrivier en Sabie in die Oos-Transvaal, ontdek het. Die plante kom volop voor in 'n klein stukkie grasveld wat deur plantasies van aangeplante denne-en bloekombome omring word. Talle ander bevolkings van die spesie is waarskynlik deur die intensiewe bosbou-aktiwiteite in hierdie gebied vernietig. Omdat hierdie Transvaalse bevolking sekere eiesoortige kenmerke vertoon (byvoorbeeld besonder harige jong blare), het die Departement Omgewingsake onlangs onderneem om die genoemde stuk grasveld teen verdere ontwikkeling te beskerm. Die moontlikheid is nie uitgesluit dat verdere vlakappelbevolkings in Oos-Transvaal en Swaziland gevind kan word nie

Habitat

Vlakappels verkies 'n sanderige grondtipe en word uitsluitlik in grasveld aangetref. Soos wat later aangetoon sal word, is vuur 'n noodsaaklike omgewingsfaktor — nie alleen vir die instandhouding van die grasveldhabitat nie, maar ook as stimulus vir die nuwe groei en blomvorming. Reënval is gewoonlik meer as 1 000 mm per jaar en in enkele gebiede kan ligte ryp in die winter voorkom.

Groeivorm

Die vlakappel is 'n dwergstruik met ondergrondse houtagtige stamme waarvan die boonste takke net benede die grondoppervlak loop. Hierdie tipe groeiwyse het tot gevolg dat uitgebreide kolonies (klone) in die veld vorm. Bogronds is die beblaarde stingels ongeveer 15-30 cm hoog. Laasgenoemde is ylvertak en dra die meestal teenoorstandig (soms afwisselend) gerangskikte blare. Die leeragtige blare is lansetvormig of ellipties met die bo-oppervlak glansend donkergroen en die onder-oppervlak 'n dowwe roomkleurige groen. Tipies vir die Myrtaceae word talle sekreetholtes (oliekliere) in die blare aangetref. Gekneusde blare het dan ook 'n kenmerkende reuk (effens soos bloekomolie).

Alhoewel immergroen, word die bogrondse dele van die vlakappel deur periodieke vure (veral gedurende die winter en vroeë lente) vernietig sodat dit telkens na 'n brand nuut uitloop. Daar is egter geen kans dat die plante in struike sal ontwikkel as hul oor 'n lang periode teen vuur beskerm word nie. Trouens, in die afwesigheid van vuur verloor die plante baie vinnig hul lewenskragtigheid en toon so te sê geen nuwe groei nie.

Die groeivorm van die vlakappel is duidelik 'n aanpassing by vuur en word ook by ander houtagtige grasveldspesies in Afrika aangetref. White (1976) is egter van mening dat hierdie tipe groeivorm primêr in reaksie op sekere grondfaktore (en nie vuur nie) ontwikkel het. Bekende voorbeelde is onder andere die klein-blinkblaar-wag-'n-bietjie (*Ziziphus zeyheriana*), grysappel (*Parinari capensis*), gousiektebossie (*Pachystigma pygmaeum*) en wilde-lemoentjie (*Salacia rehmannii*).

Blomme

Die blomme is klein, gesteeld, okselstandig en word oorwegend op die nuwe seisoen se groei gedra. Blomtyd is in die lente en die plante blom die beste wanneer nuwe groei na 'n veldbrand 'n aanvang neem. Blomkleur varieer van wit tot pienk.

Twee tipes blomme word onderskei. Sommige plante dra blomme met beide meeldrade en 'n duidelike onderstandige vrugbeginsel met styl, terwyl ander plante blomme met slegs meeldrade en geen of 'n rudimentêre vrugbeginsel en styl besit. Aanvanklik is vermoed dat eersgenoemde plante tweeslagtig en laasgenoemde manlik is ('n verskynsel bekend as andresie).

Onlangs is aanduidings gevind dat die stuifmeel van die morfologies tweeslagtige blomme steriel is en waarskynlik slegs as lokmiddel vir bestuiwers dien (geen nektar word geproduseer nie). Funksioneel is hierdie blomme dus eintlik vroulik en moet ons die vlakappel gevolglik as tweehuisig beskou (d.i. afsonderlike manlike en vroulike plante word aangetref). Vrugte word slegs deur vroulike plante geproduseer. Dit verklaar waarom sommige vlakappel-kolonies nooit enige vrugte dra nie (manlike plante).

Vrugte

Die vrugte, of te wel vlakappels, word gewoonlik van Desember tot Maart ryp. Gemiddeld word een of twee vrugte per bogrondse stammetjie gedra en die beste vrugtepro-

duksie word na 'n veldbrand verkry. Hul varieer in vorm van min of meer rond, langwerpig tot peervormig en kan tot so groot soos 'n kleinerige appel word (± 50 mm in deursnee). Dit is buitengewoon groot as die relatief tenger bogrondse groei van die spesie in aanmerking geneem word — selfs groter as die vrugte van verwante *Eugenia*-spesies wat woudbome is. Dikwels is die vrugte so groot dat die stammetjies van die plante sou buig onder die gewig daarvan, was dit nie dat hul gewoonlik net bokant grondvlak aan die stingsels vasgeheg is en gevolglik plat op die grond lê nie. Laasgenoemde posisie van die vrugte word deur die verskynsel dat blomme meestal op die nuwe groei na 'n brand gedra word, bewerkstellig.

Omdat die vrugte uit 'n onderstandige vrugbeginsel ontwikkel, is die oorblyfsels van die kelkblare blywend aan die voorpunt van die vrug. In dié opsig stem dit met vrugte soos byvoorbeeld die mispel, koejawel, granaat, peer en appel ooreen. Ryp vrugte verkleur roomkleurig, geel tot 'n aantreklike helder oranje of rooi. Hoe meer sonlig hulle ontvang, hoe rooier is die vrugte. Vrugte in die skadu is soms 'n bleekgeel kleur. Die sagte skil is glad, bevat sekreetholtes en bedek die ligte geel vrugvleis. Met uitsondering van die een of twee (selde meer) ronde sade is die hele vrug eetbaar.

Vlakappels word vars geëet en is besonder vlesig met 'n aangename en verkwikkende smaak. Die smaak is moeilik om te beskryf en is al vergelyk met dié van aarbeie, perskes en lukwarte. Geen onaangename suur nasmaak soos wat so dikwels by veldvrugte voorkom, is teenwoordig nie. Dit lyk asof vlakappels veral in die Oos-Kaap baie gewild as veldvrug was. In Natal is die vrugte besonder gewild onder die Tongas in dele van Maputaland (Van der Merwe *et al.* 1967).

Vlakappels is nie net by die mens gewild nie. Vreetmerke aan die vrugte dui daarop dat insekte, kleiner knaagdiere en waarskynlik ook voëls baie lief daarvoor is. Dit is egter nog 'n raaisel hoe die relatief groot sade in die natuur versprei word. Moontlik speel knaagdiere en bobbejane hier 'n rol.

Kweking

Die maklikste manier om vlakappels voort te plant, is deur middel van saad. Tot dusver kon ons nog nie daarin slaag om steggies te laat wortel nie. Die saad moet so gou moontlik (maar in elk geval liefs binne twee weke) nadat dit uit die ryp vrug gehaal is, geplant word. As die embrio eers eenkeer uitgedroog het, is die saad nie meer kiemkragtig nie. Om ontkieming te bespoedig, kan die harde dop (testa) versigtig verwyder word sonder om die onderliggende embrio te beskadig. Die ronde, vleisige, roomkleurig of liggroen embrio's word net onder die grondoppervlak geplant en klam gehou. Ontkiemingstempo varieer baie, maar gewoonlik word 'n bykans honderd persent ontkieming oor 'n tydperk van drie maande verkry.

Pogings om vlakappels in die botaniese tuin van die Universiteit van Pretoria te vestig, het tot dusver misluk. Ten spyte van die goeie ontkieming wat verkry is, het saailinge na 'n paar weke begin kwyn en gevrek. Daar word vermoed dat gereelde brand ook noodsaaklik is vir die suksesvolle vestiging van die vlakappel buite sy natuurlike grasveldhabitat. Hierdie vereiste is waarskynlik een van die belangrikste faktore wat kommersiële verbouing onprakties sal maak.

Voortplanting deur middel van die ondergrondse stingsels behoort ondersoek te word, omdat dit (net soos met bogrondse steggies) sal verseker dat meer vroulike plante vir vrugproduksie geplant kan word. Enkele manlike plante sal natuurlik steeds nodig wees om bestuiwing van vroulike blomme met fertiele stuifmeel te verseker, waarskynlik deur bye.

Waarom so onbekend?

Tereg kan die vraag waarom die vlakappel, ondanks al sy voortreflikhede, so onbekend is, gestel word. Een moontlike rede is dat die ryp vrugte nie oop en bloot gedra word nie. 'n Mens kan maklik deur 'n stuk grasveld stap sonder om agter te kom dat die veld om jou met vlakappels bestrooi lê. Nadat nuwe groei en blomvorming deur 'n veldbrand geïnisieer is, val ook die eerste lentereëns en begin die gras waartussen die vlakappels groei, vinnig uitloop. Teen die tyd dat die vrugte in die middel van die somer ryp is, kan die vlakappelplante beswaarlik tussen die lang gras raakgesien word. Om dan nog die vrugte te vind, moet die gras oopgedruk en op grondvlak gesoek word.

Verder is die kans ook goed dat al die gesnuffel in die lang gras niks sal oplewer nie, omdat daar dikwels meer manlike as vroulike plante in 'n gebied voorkom. Vroulike kolonies moet dus gedurende blomtyd geïdentifiseer en daarna gereeld dopgehou word om te verseker dat gediertes die ryp vrugte nie eerste ontdek nie.

Nog 'n moontlike rede waarom vlakappels nie opgemerk word nie, kan wees dat die veld in 'n gebied te lank teen vuur beskerm is. Blom- en vrugproduksie op verouderde bogrondse stingels is gewoonlik swak en kan selfs sommige jare afwesig wees. Oorbeweiding het dieselfde effek omdat verwydering van die grasstratum die kanse op veldbrand verminder. Laasgenoemde is veral in die OosKaap, Ciskei en Transkei 'n probleem.

Ander gebruike en moontlike verdere navorsing

Volgens Watt & Breyer-Brandwijk (1962) word die wortels van die vlakappel deur die Zoeloes as 'n geneesmiddel teen diarree gebruik.

Geen ander gebruike vir die plant is raakgeloop nie. Dit is ook nie bekend of die vrugte al vir die kook van konfyt of in ander resepte gebruik is nie. Die outeur sal enige verdere inligting oor die vlakappel waarvan lesers mag weet, besonder waardeer.

Mnr A. B. Cunningham, Departement Plantkunde, Universiteit van Kaapstad, het onlangs 'n omvattende ondersoek van plantgebruike in Maputaland onderneem. Die vlakappel kom ook hierin ter sprake en 'n publikasie oor sy bevindings word in die vooruitsig gestel. Dit sal onder andere inligting rakende die voedingstofsamestelling van die vrugte bevat.

Op smaak geoordeel, is die vlakappel een van die beste (indien nie dié beste) veldvrugte in Suider-Afrika. Die moontlike veredeling van die vlakappel behoort ernstig ondersoek te word. Variasie in vruggrootte dui daarop dat veldwerk reeds voortreflike plante met vrugte wat aansienlik groter as die gemiddelde is, kan lewer.

Summary

The "vlakappel" or "myrtle apple" (Eugenia albanensis, *family Myrtaceae) is a rhizomatous geoxylic suffrutex which is common in grassveld along the east coast of southern Africa, particularly in Natal. Despite its edible fruits, which were great favourites among colonists and native tribes, it is still surprisingly poorly known.*

New growth and subsequent flowering is stimulated by fire in late winter and spring. Small white or pinkish flowers are borne mainly in the first few axils of the new season's growth. Morphologically these are two types, viz. apparently hermaphrodite (stamens and well developed inferior ovary with style present) and male (stamens present but ovary and style absent or rudimentary). However, pollen of the former type appears to be sterile and the species is therefore considered to be functionally dioecious (separate male and female plants).

Fruits are usually produced at or near ground level and ripen in summer. They resemble small apples or pears (up to 50 mm in diameter) and are usually a bright orange to red with yellowish flesh and one or two (rarely more) roundish seeds. Although relatively large and conspicuous, the fruits are usually concealed by grass and are therefore not readily encountered unless deliberately sought. Eaten fresh they are delicious with a unique refreshing taste — according to some authors reminiscent of strawberries, peaches or loquats. The possibility of introducing the plant into cultivation should be seriously considered.

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11.3.6 ***Eugenia erythrophylla*** Strey in Bothalia 10(4): 569 (1972). Type: Transkei, 3129 (Port St. Johns): Goss Point (–BD), *Strey & Nicholson* 10100 (NH, holo.!; PRE, iso.!).

This is a distinctive species characterized by thick leathery leaves up to 170 mm long and 110 mm wide (the largest leaves of the native eugenias), structurally hermaphrodite flowers with the hypanthium obconical and densely tomentose, flowers occasionally sessile and young shoots and leaves which are densely tomentose to villous—even up to the stage when the leaves are fully expanded. The specific epithet alludes to the bright red colour of the new leaves—a phenomenon often displayed by the species of particularly species group Y (brownish-red in group X). *E. erythrophylla* is a medium to large sized tree endemic to the sandstone region of southern Natal and Pondoland. Previous reports of the species in northern Natal are based on misidentified specimens of *E. woodii* subsp. *woodii*.

Plants growing in exposed habitats occasionally have relatively smaller leaves and could then be confused with sterile specimens of *E.* sp. B. Young leaves in the latter species are, however, sericeous and the indumentum is fairly ephemeral. For additional distinctions see under E. sp. B (11.3.13).

FIGURE 8, page 221.

REPRESENTATIVE SPECIMENS: *Van Wyk* 3342, 4231, 4237, 4238, 4338, 4511, 5028, 5289, 6091, 6103; *Van Wyk & Venter* 1312, 1348 (all in PRU).

11.3.7 ***Eugenia pusilla*** N.E. Br. in Kew Bull. 1912: 276 (1912). Type: Transvaal, near Amsterdam, in Ermelo district, *Forbes* s.n. ex PRE 6748 (K, holo.).

E. pusilla is a rhizomatous geoxylic suffrutex recorded in 1911 and now probably extinct. Numerous excursions to relocate the species were unsuccessful. Neither did a request in a regional newspaper elicit any knowledge of the species. Apparently it used to be fairly well-known to local inhabitants because it was suspected to be the cause of sheep poisoning. The original gatherings were made during March 1911 by Miss M.O. Forbes and later also by Mr. J. Forbes of the farm Athole near Amsterdam in the eastern Transvaal. It should be noted that the plants were apparently not collected on Athole, but at an unknown locality in the Piet Retief district (most probably near the Swaziland border). This possibility was overlooked by previous authors who took the address of Miss Forbes (later Mrs. Dunn) as the collection site. The type locality supplied above (quoted from Brown 1912) could therefore be incorrect. Three specimens of the plant were retained at PRE (accession numbers 6350, 6367 & 6385, allocated in March 1911). These were mounted on a single sheet numbered PRE 6350. All three specimens are sterile. The material used by Brown to draw up the species description was from a later gathering made December, 7, 1911. (PRE 6748, but apparently no duplicates in PRE). Since flowers are described, the collection must have been fertile. The following note is attached to the sheet in PRE—note that it is specifically mentioned that the plants are from the Piet Retief District:

POISONOUS PLANTS FROM M.O. FORBES, ATHOLE

6350. Eugenia pusilla N.E. Br. 'Lomo' sp. nov.

Native medicinal plant. Also supposed to be a deadly poison to sheep and goats. Natives know that if goats or sheep feed even for half an hour on certain ridges some of them will die but very few of them know what kills them (or think they know). Plants come from Piet Retief District. Natives say the flower is small and insignificant but fruit a red fleshy berry with a seed like stem-fruit. As a preventative they pound up roots and leaves, pour hot water on and give the animal 'a little' (they say) every morning for a month. They say it is better not at all fresh. This preventative lasts 3 years and then the goats have to be re-dosed.

Plants are most deadly they say from January to March or April, or till the frost comes.

NOTE: There is no proof that any of the native species of *Eugenia* is poisonous. The poisoning of sheep and goats mentioned above, could have been caused by *Pachystigma pygmaeum* (Schltr.) Robyns (Rubiaceae).

E. pusilla is a distinctive species on account of its very narrow leaves. It is apparently related to *E. albanensis*, but to date no intermediate specimens linking the two species have been found. Even the outlier populations of *E. albanensis* recently discovered in the eastern Transvaal match the fairly broad-leaved plants from Natal. There is nevertheless still a strong possibility that *E. pusilla* is just a narrow leaved variant of *E. albanensis*. In such a case subspecific rank under the latter species should be considered for it. For the present, and pending further efforts to locate living plants, *E. pusilla* is maintained at the species level.

E. pusilla N.E. Br. var. *latior* Duemmer in Gdnrs' Chron. ser. 3, 52: 198 (1912) may be a large leaf variant of *E. pusilla*. It is based on a specimen, *Gerrard* 1645. Duemmer (1912) cited the locality as 'Natal; without precise locality'. I have seen a specimen from Kew, determined by F. White in 1975 as the isotype of the aforementioned variety name. It consists of a scrap with leaves *ca.* 4 mm wide, 35 mm long and with a single flower subtended by two foliaceous bracteoles. These bracteoles are not mentioned by Duemmer. They are, however, so conspicuous that I doubt whether Duemmer saw this particular sheet (this is quite possible if it is indeed an isotype). There is also a note attached to the sheet giving the origin of the plant as 'collected by Dr. Toohly in Amaswasiland 200 miles or more, north

of the Colony'. Gerrard's collection number could be read either as 1645 or 1643. There is some doubt as to whether this collection is really a duplicate of *Gerrard* 1645. I have decided to provisionally consider *E. pusilla* var. *latior* insufficiently known. It may be significant that in southern Africa foliaceous bracteoles are occasionally present in *E. albanensis*. If the specimen referred to above is indeed an isotype for var. *latior*, it would strengthen the suspected affinity between *E. pusilla* and *E. albanensis*.

FIGURE 9, page 222.

REPRESENTATIVE SPECIMENS: *Forbes* s.n., sub PRE 6350 (PRE).

11.3.8 ***Eugenia verdoorniae*** Van Wyk in Jl S. Afr. Bot. 45(3): 273 (1979). Type: Transkei, 3129 (Port St.Johns): Mkweni River mouth S. of Goss Point (–BD), *Van Wyk* 1614 (PRE, holo.!).

E. verdoorniae is a distinctive species unlikely to be confused with any other native member of the genus. It is an attractive, much branched and densely leaved shrub or small tree up to 5 m tall. The species is endemic to the sandstone region of southern Natal and Pondoland. Plants grow in fairly moist forest or between rocks on the banks and islands of rivers. It has been recorded as growing sympatrically with *E. erythrophylla, E. umtamvunensis, E. natalitia, E. simii* and *E.* sp. C. *E. verdoorniae* is unique in being the only native species of *Eugenia* which flowers mainly in winter (June & July). The species is no longer considered andromonoecious (see Van Wyk & Lowrey; page 133). For a detailed description and notes on diagnostic features see Van Wyk (1979); page 201.

FIGURE 1, page 204 and FIGURE 10, page 223.

REPRESENTATIVE SPECIMENS: *Abbott* 270, 1016; *Schrire, Van Wyk & Abbott* 1774, 1816; *Van Wyk* 1615, 1616, 1617, 1622, 1682, 2334, 2335, 3282, 3284, 4503, 4512, 6111, 6124 (all in PRU).

Jl S. Afr. Bot. 45 (3): 273–277 (1979)

A NEW SPECIES OF *EUGENIA* L. (MYRTACEAE) FROM SOUTHERN NATAL AND TRANSKEI

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ABSTRACT

Eugenia verdoorniae Van Wyk, a new species from Southern Natal and Transkei is described.

UITTREKSEL

'n NUWE *EUGENIA*-SPESIE (MYRTACEAE) VAN SUID-NATAL EN TRANSKEI

Eugenia verdoorniae Van Wyk, 'n nuwe spesie van Suid-Natal en Transkei word beskryf.

INTRODUCTION

While working on the South African Myrtaceae a need was felt for a specific name to refer to a still unnamed *Eugenia* species which has been discovered after the revision of Dümmer (1912).

The purpose of this article is to describe this species which was first collected in 1925 in the Lusikisiki district of Transkei. Between 1925 and 1929 several herbarium specimens of it were sent to Pretoria by Mr G. Fraser, a forester stationed at the Ntsubane forest station in Transkei.

These specimens were studied by Dr I. C. Verdoorn of the Botanical Research Institute. She recognised them as belonging to a new species and, during the 1930s, prepared a preliminary description which was, however, never published. The name *E. fraseri* (after its discoverer) was proposed. Unfortunately this name was at that time already used for a *Eugenia* species from Borneo.

Field observations and evidence from a recent anatomical investigation (Van Wyk, 1978) confirm the distinctness of this species. I thus take pleasure in naming it after Dr Verdoorn in recognition of her contribution to the taxonomy of South African plants.

DESCRIPTION

Eugenia verdoorniae Van Wyk, sp. nov., species haec a ceteris speciebus Africae australis differt foliis perangustis et planis, margine non revoluto, costa in

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statu vivo utrinque obsoleta, in statu sicco autem supra leviter canaliculata in inferiore triente tantum, infra passim valde elevata.

Est affinis illis speciebus Africae australis quae exhibent semen globosum, testam crassam lignosamque, et embryonem non conspicue glandulis punctatum.

Evergreen, androdioecious or andromonoecious, much-branched shrub or small tree, 1–3 m tall; branched from the base or with a single trunk up to 200 mm diam.; young branches reddish-brown to brown becoming grey when mature, sparingly covered with inconspicuous appressed hairs, branchlets becoming glabrous with age; internodes (4–)6–12(–20) mm long. *Leaves* decussate, petiolate; lamina dark red or pinkish when young, becoming dark green and shiny above, paler and dull below, glandular-punctate, initially covered with inconspicuous appressed hairs (especially basal third of lamina), becoming glabrous with age, narrowly elliptic to narrowly linear-lanceolate, (15–)20–40(–45) mm long, (4–)5–6(–8) mm wide, apex acute or obtuse, gradually tapering from the middle into a short petiole; venation pinnately netveined, midrib in dried leaves flat or slightly concave for basal third of length above, strongly elevated below, flat on both sides in fresh leaves; primary lateral veins alternate or opposite, 4–6 pairs, spreading, obscure above but raised below in dried leaves, obscure on both sides in fresh leaves, fused into a longitudinal slightly lobed marginal vein about 0,5 mm from the margin of the lamina, tertiary veins obscure; blade coriaceous, flat, margin entire and slightly revolute only in dried leaves; petiole 1–2 mm long, ventrally slightly canaliculate. *Inflorescences* usually short axillary few-flowered leafless racemes which often develop as leafy shoots, the number of flowers in a raceme sometimes reduced to one or two, flowers rarely solitary, sparingly pubescent; bracts often caducous. *Staminate flowers* subsessile or with pedicels 3–5 mm long, bracteoles 2, attached at the base of the hypanthium, 0,5–1 mm long, 0,3–0,4 mm wide, acute, erect, sparingly pubescent mainly on the margins. *Sepals* 4, subrotund, 2 large, 1–1,5 mm long, 1,8–2,5 mm wide, 2 small, 0,5–1,3 mm long, 1,5–2,0 mm wide, glabrous except for a few hairs on the margins, the abaxial surface sp`ringly gland-dotted. *Petals* 4, free, white, sometimes with a tinge of pink, more or less oval, c. 3–4 mm long, 2,5–4 mm wide, margins not ciliate, sometimes with a few (c. 5) scattered glands. *Disc* flat with a central depression, surface wrinkled, fleshy, sparingly pubescent. *Stamens* (14–)16–20(–22), arising from the disc; filaments of various lengths, (3–)4–5(–6) mm long, free to the base; anthers 2—thecous, each theca opening with a longitudinal slit, versatile, c. 1 mm long, 0,6–0,8 mm broad, all fertile. *Hypanthium* more or less obconical, c. 1 mm long, glabrous. *Ovary* abortive; style rudimentary, 0,5 mm long; stigma absent. *Bisexual flowers* subsessile or with pedicels 3–5 mm long; bracteoles as in staminate flowers. *Sepals* and *petals* as in staminate flowers. *Disc* flat with an even surface, fleshy, sparingly pubescent. *Stamens* (11–)14–16(–20), resembling those of the staminate flowers. *Hypanthium* obconical, 1,5–2

mm long. *Ovary* fused to the lower part of hypanthium, 2–3 locular; ovules (1–)2(–4) per locule, 1 or 2 developing; style filiform, terete, glabrous, 4–5 mm long; stigma small, slightly discoid, covered with small papillae. *Fruit* a fleshy red? (known only from dried specimens) berry, obovoid to subglobose, c. 18 mm diam., glabrescent with persistent calyx lobes at the apex; pericarp closely adhering to the testa—but not fused with it. *Seed* globose with a smooth surface, c. 10–15 mm diam.; testa woody and tough with a fibrous texture, c. 0,5 mm thick, light brown; embryo with cotyledons partly fused, light green and fleshy, not conspicuously glandular-punctate.

Flowering throughout the year, but mainly from June to July.

Type: Transkei—3129 (Port St. Johns): Mkweni river mouth, S. of Goss Point (-BD), *Van Wyk 1614* (PRE!, holo.).

Distribution

Since its discovery, and especially during the last ten years, sporadic collections of *E. verdoorniae* have been made. The species seems to have a rather restricted distribution in Southern Natal and Pondoland where it is confined to a few scattered localities in the districts of Lusikisiki, Bizana and Port Shepstone. It usually grows on the margin of natural forests or in the open on the banks and islands of some of the larger rivers. Although common in some localities, it is a rare species in need of protection.

Specimens Examined

NATAL—3030 (Port Shepstone): Umtamvuna nature reserve (-CC), *Moll 5490* (PRE, NH); Umtamvuna river, *Nicholson 896* (PRE); Beacon Hill West, *Strey 7227* (NH), *Van Wyk 1681, 1682, 1696, 1700* (PRE, PRU).
TRANSKEI—3129 (Port St. Johns): Indindinde stream, below Indindinde Drift (-BD)?, *Frazer Z. 34* (PRE), *s.n.* sub PRF *7353* (PRE); Indindinde forest, *Fraser s.n.* sub PRF *6054* (PRE); Mkweni river mouth, S. of Goss Point (-BD), *Nicholson 941* (PRE), *Van Wyk 1614*, (PRE!, holo.) *1615, 1616, 1617* (PRE, PRU); Msikaba river mouth, *Van Wyk 1622* (PRE, PRU); Goss Point, *Strey 10157* (PRE, NH).

Discussion

E. verdoorniae (Fig. 1) can easily be distinguished from the other Southern African *Eugenia* species by the following combination of characteristics: (i) narrow flat leaves with the margin not revolute; (ii) the midrib flat on both sides in fresh material; (iii) the midrib only slightly concave above, but raised below in dried leaves; (iv) seeds globose, testa thick and tough; (v) the embryo not

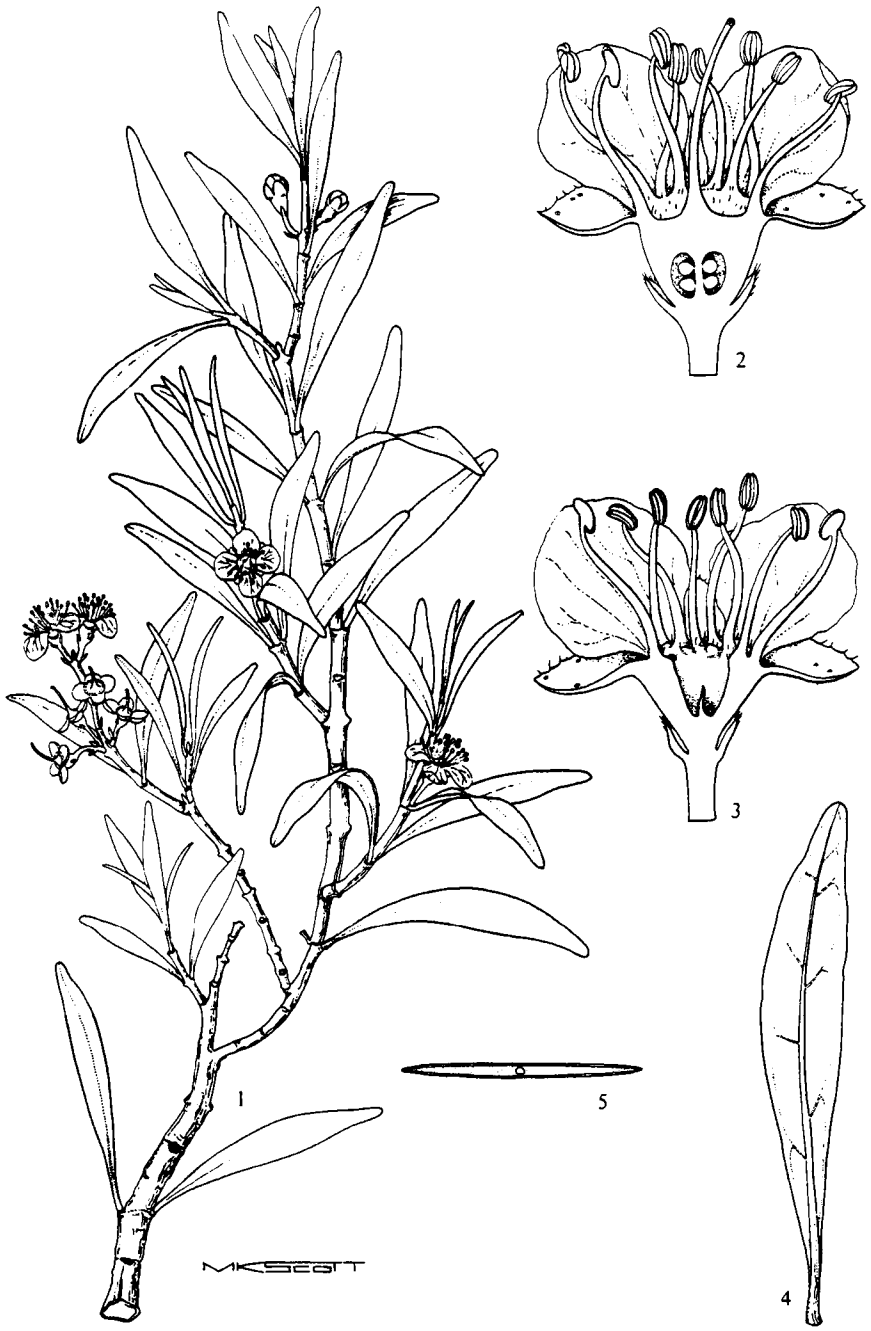

FIG. 1.
Eugenia verdoorniae. 1, leafy twig with flowers, × 1; 2, longitudinal section of bisexual flower, × 6 (both from *Van Wyk 1614*); 3, longitudinal section of male flower, × 6 (*Van Wyk 1615*); 4, leaf to show veination, × 2; 5, transection of fresh leaf, × 6 (both from *Van Wyk 1614*).

conspicuously glandular-punctate; (vi) stems in which the first-formed periderm originates in the primary external phloem.

It is related to the group of species (Group Y, vide Van Wyk, 1978) that includes *E. woodii, E. zuluensis, E. albanensis, E. zeyheri, E. pusilla* and *E. erythrophylla*.

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11.3.9 ***Eugenia woodii*** Duemmer in Gdnrs' Chron. ser. 3, 52: 192 (1912). Syntypes: Natal, without precise locality, *Gerrard* 1643 (K!); between bushes near Durban, *Wood* 132 (K, syn.!; BM, PRE, isosyn.!).

E. woodii is a widespread tree of coastal and inland forest regions. Diagnostic characters include the often hairy young leaves, and flowers with the hypanthium densely sericeous and borne in usually 3-flowered cymules. *E. albanensis* is the only other native species of *Eugenia* for which cymules have been recorded. For an amplified description and additional diagnostic features see Van Wyk (1980); page 207.

Van Wyk (1980) hinted that a thorough study of the fresh fruits of *E. woodii* may eventually prove that the species can be separated into several infraspecific taxa. Subsequent work has shown that variations in the size and shape of the fruits are mainly caused by insect infestation. Vegetative characters nevertheless allowed the recognition of two subspecies.

Key to the subspecies of *E. woodii*

1 Leaves more or less obovate to spathulate, rarely elliptic; secondary veins curved apically and not with a tendency to be arranged at right angles to the primary vein, plane or slightly elevated on the upper surface of the lamina; young leaves and shoots densely sericeous, soon becoming glabrous; trees recorded from coastal forest in Natal and ranging north into the FZ region . . . . . 11.3.9.1. subsp. *woodii*

1 Leaves more or less broadly elliptic to elliptic; secondary veins arranged almost at right angles to the primary vein, occasionally conspicuously elevated on the upper surface of the lamina; young leaves and shoots often densely tomentose, indumentum fairly persistent; trees recorded from Swaziland, Venda and the Transvaal . . . . . 11.3.9.2. subsp. A

11.3.9.1 ***E. woodii*** Duemmer subsp. ***woodii***

E. capensis (Eckl. & Zeyh.) Sond. subsp. *natalitia* (Sond.) F. White in Kirkia 10: 402 (1977) pro parte. Type as for *E. natalitia* Sond.

The typical subspecies is a forest tree in the coastal zone of Natal. In the past it has often been confused with *E. natalitia* (see Van Wyk 1980; page 207). Subsp. *woodii* does not occur south of Port Shepstone. The most southerly population known is at Umdoni Park, between Pennington and Sezela. Vegetative material from this locality is indistinguishable from *E.* sp. C. However, specimens in flower clearly reflect the separate status of the two taxa. Flowers in *E.* sp. C are not disposed in 3-flowered cymules but are solitary, or rarely in short axillary racemes. The hypanthium is essentially glabrous (occasionally very sparingly appressed pubescent)—never densely sericeous as in *E. woodii*. On account of its flaky bark surface, subsp. *woodii* has also been confused with *E. zuluensis*. However, the latter species is confined to the more temperate mist belt forest further inland and does not occur near the coast. In addition, the midrib is conspicuously raised on the upper lamina surface, whereas it is more or less plane in *E. woodii*. Flowers are solitary in *E. zuluensis*.

Subsp. *woodii* ranges north into the FZ region. I can confirm its presence in Mozambique (Manica and Sofala) (*Müller* 3735 & 3736 in PRU & SRGH). Leaves of these plants are much larger than those from their southern counterparts.

FIGURE 11, page 224 and FIGURE 13, page 208.

REPRESENTATIVE SPECIMENS: *Botha & Van Wyk* 949, 1122; *Lowrey & Van Wyk* 1024, 1041; *Van Wyk* 2517, 2522, 4255, 5044, 5045, 5047, 5058; *Venter* 5573, 5913, 6099 (all in PRU).

11.3.9.2 ***E. woodii*** Duemmer subsp. **A**

?E. capensis (Eckl. & Zeyh.) Sond. subsp. *natalitia* (Sond.) F. White in Kirkia 10: 402 (1977) pro parte. Type as for *E. natalitia* Sond.

Subsp. A replaces subsp. *woodii* in the more temperate escarpment forests of Swaziland and the Transvaal, including Venda. It is common in the forest areas of the Soutpansberg. This subspecies is much more hairy than subsp. *woodii*. The indumentum on the young leaves is tomentose and fairly persistent, not sericeous as in subsp. *woodii*. The tomentose young leaves are strongly reminiscent of *E. erythrophylla* from southern Natal and Pondoland. *E. woodii* subsp. A is the 'unnamed' species of *Eugenia* with the '8–10 pairs of fine lateral veins running outwards at right angles to the midrib' mentioned by Palmer & Pitman (1972, p. 1667). This subspecies often grows sympatrically with *E. natalitia*. Together with *E. zuluensis* (which is rare) they represent the only tree forms of *Eugenia* in the forests of the Transvaal. The line drawing in Van Wyk 1980 (Figure 14; page 210) depicts *E. woodii* subsp. A.

FIGURE 12, page 225 and FIGURE 14, page 210.

REPRESENTATIVE SPECIMENS: *Van Wyk* 825, 826, 905, 907, 2146, 2150, 2165, 2168, 2419, 2698, 2805, 3761, 3869, 4061, 4063; *Van Wyk & Theron* 4632, 4873; *Venter* 10463 (all in PRU).

THE IDENTITY OF *EUGENIA WOODII*

in

NOTES ON AFRICAN PLANTS : MYRTACEAE

by

A.E. VAN WYK

BOTHALIA 13: 142–145 (1980)

MYRTACEAE

THE IDENTITY OF *EUGENIA WOODII*

Ever since *Eugenia woodii* Dümmer (1912) was described, some doubt has existed as to whether it is a distinct species. In his original diagnosis Dümmer distinguished *E. woodii* from *E. zuluensis* Dümmer by its broadly elliptic or obovate leaves with the midrib impressed above (prominently raised in *E. zuluensis*) and the hypanthium covered with white appressed hairs. He also noted that the ultimate branchlets were slightly sericeous towards their apices, while the axillary and apical buds were appressedly pubescent.

Engler and Von Brehmer (1917) included *E. woodii* in their enumeration of African Myrtaceae, but did not mention some of the outstanding features of this species. In fact, they described the branches and the hypanthium as being glabrous, a character not found on any of three specimens of the syntype, *Wood* 132, investigated by the present author (Fig. 13).

Examination of the material of *Eugenia* in the National Herbarium, Pretoria and the Natal Herbarium, Durban, revealed that almost all the specimens of *E. woodii* were misidentified. Most material was placed under *E. natalitia* Sond., but some specimens from the Transvaal were not identified to species. Three specimens in the National Herbarium, however, were correctly identified as *E. woodii* by Dr G. J. H. Amshoff of Wageningen in 1960 or 1961 and have apparently escaped the attention of subsequent workers. Dr Amshoff was obviously aware of the correct identity of *E. woodii*, as she had previously referred to the characteristically 2–3-flowered "pedicels" of this species in one of her papers (Amshoff, 1958).

The confusion of *E. woodii* with *E. natalitia* probably arose because of the superficial resemblance in leaf shape. Because of the undue emphasis placed upon leaf shape, the taxonomic significance of the pubescence and other characters of *E. woodii* was apparently either ignored or treated as trivial in nature. This probably led to the inability to distinguish between the two species, and the subsequent incorporation of *E. woodii* as a synonym under *E. natalitia* by Palmer & Pitman (1973). This concept was taken one step further by White (1977), who also added *E. zuluensis* as a synonym and at the same time reduced *E. natalitia* to the

FIG. 13.—*Eugenia woodii*. Part of the syntype, *Wood* 132 (BM), showing the densely pubescent hypanthia (A) and characteristically 3-flowered cymules (B).

status of subspecies, viz. *E. capensis* (Eckl. & Zeyh.) Sond. subsp. *natalitia* (Sond.) F. White.

The present study has shown that *E. woodii* is a very distinct species, which is not closely related to *E. natalitia*. The comparative anatomy (Van Wyk, 1978) and external morphology revealed additional distinguishing characters which had hitherto been overlooked. Some of these are now included in Table 1, which will enable one to distinguish most specimens of *E. natalitia* and *E. woodii*.

It must be emphasized that morphological characters in the genus *Eugenia* are extremely variable. Taxonomic conclusions must therefore be based on as many different characters as possible. The most reliable characters that can be used to distinguish between the two species are the nature of the disc in bisexual flowers, the degree of pubescence of the hypanthium, the nature of the seeds and the position of the first-formed periderm in the stem. By using the phloroglucinol/hydrochloric acid test on freehand sections of fresh or rehydrated material, the nature of the periderm can be ascertained quickly and easily.

Although *E. woodii* shows some similarity to *E. zuluensis* Dümmer, *E. albanensis* Sond., *E. zeyheri* Harv. and *E. pusilla* N.E. Br., it seems to be more closely related to the recently described *E. erythrophylla* Strey from southern Natal and Transkei, with which it is sometimes confused. However, *E. erythrophylla* differs from *E. woodii* in its more coriaceous and often larger leaves and the much larger flowers, which are usually shorter pedicellate and not aggregated in 3-flowered cymules. The young leaves of *E. erythrophylla* are often densely whitish pilose on both sides with the upper surface of the lamina usually becoming glabrous before the lower; the reverse is found in *E. woodii*. The pubescence on the hypanthium of *E. erythrophylla* also tends to be denser and more spreading than that of *E. woodii*.

The following amplified description of *E. woodii* is based on the more abundant material now at hand.

Eugenia woodii *Dümmer* in Gdnrs' Chron. ser.3, 52: 192 (1912); Engl. & Von Brehmer in Bot. Jb. 54: 333 (1917); Von Breitenbach in Indig. Trees S. Afr. 4: 845 (1965). Syntypes: Natal, without precise locality, *Gerrard* 1643 (K!); between bushes near Durban, *Wood* 132 (K!; BM!; PRE!).

Eugenia natalitia sensu Palmer & Pitman in Trees S. Afr. 3: 1669 (1973), pro parte quoad *E. woodii*; sensu Compton in Fl. Swaziland: 396, pro parte quoad *Compton* 25175.

Eugenia capensis (Eckl. & Zeyh.) Sond. subsp. *natalitia* (Sond.) F. White in Kirkia 10: 402 (1977), pro parte quoad *E. woodii*; sensu Coates Palgrave in Trees S. Afr.: 689, pro parte.

Tree up to 20 m high. *Bark* dark brown to grey or whitish, corky and rough, typically flaking off in irregular pieces. *Branchlets* reddish-brown to brown becoming grey when mature, flattened, sparingly to densely covered with appressed hairs, and glabrascent later; buds densely pubescent; internodes (10–) 20–40 (–55) mm long. *Leaves* decussate, rarely in threes, petiolate, lamina conspicuously bronze or pinkish when young, becoming dark green and shiny above, pale whitish green and dull below, initially densely whitish pilose above, usually sparingly pilose to glabrous beneath, soon becoming glabrous with age, usually elliptic to broadly elliptic or obovate to broadly obovate, 35–90 mm long, 20–60 mm wide, with apex bluntly or obtusely cuspidate, tapering from about the middle into the petiole, coriaceous, with revolute margin in dried and fresh leaves; venation pinnately net veined, midrib in dried leaves deeply concave above, strongly elevated below, concave above and prominently elevated below in fresh leaves; primary lateral veins alternate or opposite, (6–) 8–12 (–14) pairs, spreading, raised on both sides in dried leaves, slightly raised or flat on both sides in fresh leaves, fused into a longitudinal lobed marginal vein about 1–4 mm from the margin of the lamina; tertiary veins slightly raised on both sides in dried leaves, obscure in fresh ones; petiole (4–) 5–8 (–10) mm long, ventrally canaliculate and sometimes sparingly covered with appressed hairs. *Inflorescences* rarely short 2–4-flowered racemes mainly on the older wood, flowers usually solitary of in 3-flowered cymules in the axils of bracts or leaves on the first few nodes of the new seasons growth. *Staminate flowers* usually with pedicels (3–) 8–15 (–20) mm long; bracteoles 2, attached at the base of the hypanthium, often absent in the lateral flowers of a 3-flowered cymule, about as long as the hypanthium, c. 0,4–0,8 mm wide, lanceolate, acute, usually densely appressed pubescent, eglandular or with 1–4 glands. *Sepals* 4, subrotund with the apices tending to be acute, 2 large, c. 1,5–2 mm long, c. 2 mm wide, 2 small, c. 1–1,5 mm long, c. 1,5 mm wide, outer surface sparingly to densely pubescent and sparingly gland-dotted, margins usually ciliolate. *Petals* 4, very rarely 5, white to greenish-white or pinkish, usually elliptic, sometimes oblong or more or less oval, c. 4–6 mm long, c. 3–4 mm wide, margins usually ciliolate, eglandular or with a few obscure glands. *Disc* with a central depression, surface even, fleshy and usually densely pubescent. *Stamens* usually 20–30, arising from the disc; filaments of various lengths, c. 3–6 mm long; anthers 2-thecous, 1×0,75 mm, all fertile. *Hypanthium* more or less

TABLE 1.—Organographic and anatomical differences between *Eugenia woodii* and *E. natalitia*. Characters regarded as most significant are marked with an asterisk

Character	*E. woodii*	*E. natalitia*
Bark	Rough and corky, usually flaking in irregular pieces	Usually smooth or slightly rough, sometimes lightly flaking
Pubescence of apical and axillary buds	Densely pubescent	Very sparingly pubescent or glabrous
Pubescence of the lamina in young leaves	Densely pubescent above, sparingly pubescent and soon becoming glabrous beneath	More or less glabrous on both surfaces
Nature of the abaxial lamina surface in mature leaves	Dull whitish-green; secretory cavities usually obscure	Dull green; usually conspicuously glandular punctate
Inflorescences	Flowers usually solitary or in 3-flowered cymules, rarely in racemes	Flowers usually in short racemes (often fasciculate) or solitary, very rarely in cymules
Shape, length and surface of the bracteoles	Lanceolate, acute, c. as long as the hypanthium, densely pubescent	Deltoid, concave, c. ¼–½ the length of the hypanthium, sparingly pubescent or glabrous
*Surface of the hypanthium	Densely covered with whitish appressed hairs	Glabrous
Nature of the sepals	Usually more or less acute, slightly concave; margins usually ciliolate	Rounded, prominently concave; margins usually smooth or with a few scattered hairs
Nature of the petals	White or pinkish, eglandular or with a few obscure secretory cavities; margins ciliolate	White, conspicuously dotted with large secretory cavities; margins smooth or with a few scattered hairs
*Nature of the disc in bisexual flowers	Convex, densely pubescent between the stamens	Plane, sparingly pubescent between stamens
Number of stamens in bisexual flowers	Usually 10–20	Usually 30–50
Fruits	Red; flesh cream-coloured	Usually purple, sometimes red; flesh thinner and white
*Seeds	More or less globose; testa thick and woody (c. 1 mm); embryo apparently eglandular	More or less reniform to subreniform; testa thin (c. 0,25 mm) and membranous; embryo conspicuously glandular punctate
*Position of the first-formed periderm in the stem	Subepidermally in the cortex	Deeply seated in the primary external phloem to the inside of the extraxylary ring of fibres

obconical, c. 1–2 mm long, densely appressed pubescent. *Ovary* aborted; style rudimentary, sometimes split into two, c. 0,5–1 mm long or absent; stigma absent. *Bisexual flowers* with the pedicels, bracteoles, *sepals* and *petals* as in staminate flowers. *Disc* convex with an even surface, fleshy, usually densely pubescent. *Stamens* usually 10–20, resembling those of the staminate flowers. *Hypanthium* obconical, c. 2 mm long, covered with whitish appressed hairs. *Ovary* fused to the lower part of the hypanthium, 2- locular; ovules usually 2 per locule, 1 or 2 developing; style filiform, terete, glabrous or with a few scattered hairs, c. 4–6 mm long; stigma small, somewhat capitate, covered with small papillae. *Fruit* a fleshy berry, at first yellow, becoming bright red when ripe, obovoid to subglobose, c 15–25 mm diam., glabrescent with persistent calyx lobes at the apex; flesh of pericarp reported to be cream-coloured. *Seed* globose with a smooth surface; testa woody and tough with a fibrous texture, c. 1 mm thick, brownish; embryo with cotyledons partly fused, apparently eglandular but sometimes with a few obscure glands mainly associated with the radicular protuberance. Fig. 14.

E. woodii occurs as a tree in forest and associated woodland in Natal, Transvaal and Swaziland probably extending into Mozambique. It is locally common in some localities, especially the forests of the north and north-eastern Transvaal where it often occurs in association with *E. natalitia* Sond. Flowering takes place mainly from September to November.

For the present I am referring to *E. woodii* all the specimens (mainly from PRE and PRU) cited below. Unfortunately most collections are without bisexual flowers or fruits, therefore these identifications must be considered as tentative. There are indications that a thorough study of the fresh fruits of *E. woodii* may eventually prove that the species can be separated into several infraspecific taxa.

TRANSVAAL.—2229 (Waterpoort): Wylliespoort (–DD), *Van Wyk 903*; *904*; *905* (PRU). 2230 (Messina): Entabeni (–CC), *Poynton s.n. sub PRE 50706* (PRE); Tate Vondo Forest Reserve (–CD), *Hemm 22* (PRE). 2329 (Pietersburg): Lejuma near Louis Trichardt (–AB), *De Winter 6003A*; Hanglip Forest Reserve (–BB), *Poynton s.n. sub PRE 50630* (PRE), *Van Wyk 907* (PRU). 2430 (Pilgrim's Rest): 10 km from the Ofcolaco–Trichardtsdal junction on the road to the Downs (–AA), *Van Wyk 2168* (PRU); Cyprus Farm (–AB), *Renny 182*; *226*; *245* (PRE); *Van Wyk 2165* (PRU); Welgevonden Forest Reserve (–DB), *Loock s.n. sub PRE 57403* (PRE); Blydepoort Nature Reserve (–DB), *Botha 1972* (PRU; PUC); *Van Wyk 825* PRU); Mariepskop, near Reitz's grave (–DB), *Van der Schijff 6013* (PRE; PRU); Mariepskop, Blyde River picnic spot (–DB), *Van der Schijff 6091*, *6394A* (PRE; PRU); *Van Wyk 2146*; *2150* (PRU); Lothian Forest near Bushbuck Ridge (–DD), *Forest Officer 35* (PRE). Grid. ref. unknown: Soutpansberg Mountains, *Poynton s.n. sub PRE 50653* (PRE).

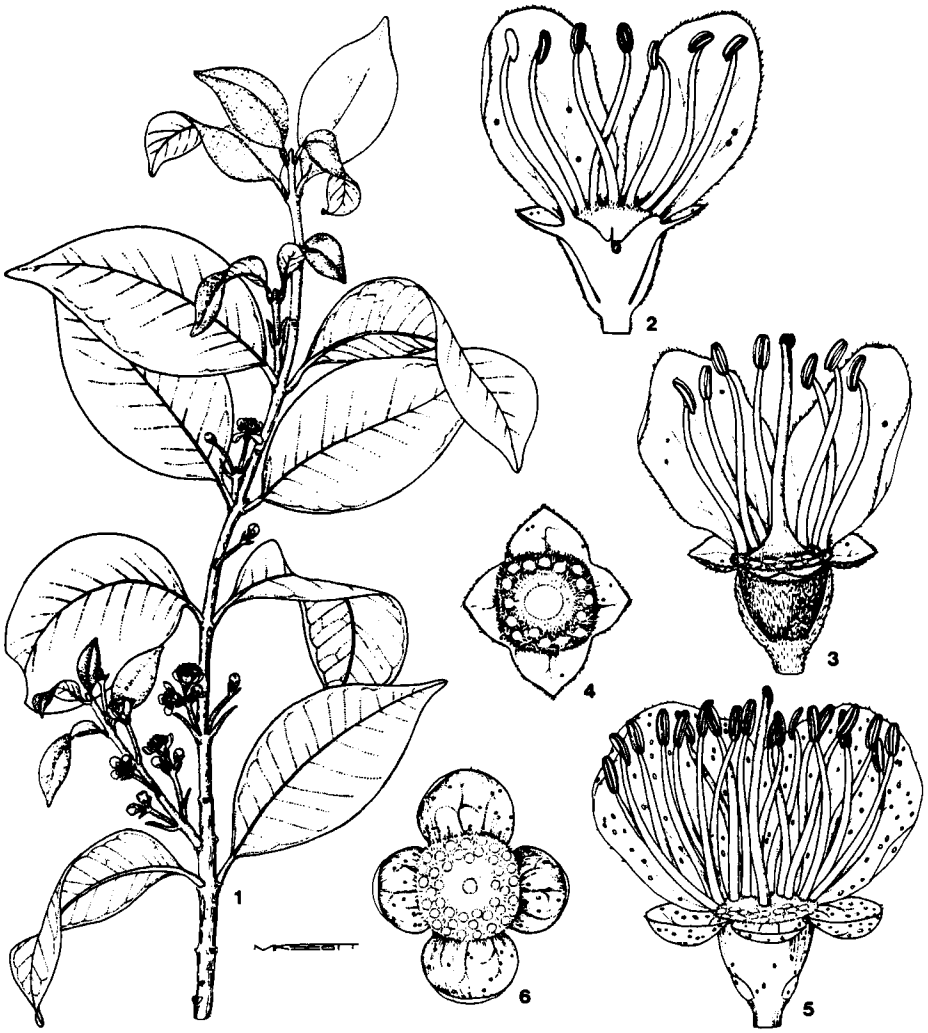

FIG. 14.—*Eugenia woodii* compared with *E. natalitia*. *E. woodii*: 1, leafy twig with male flowers, ×0,5; 2, longitudinal section of male flower, ×6; 3, bisexual flower with front petals and stamens removed, ×6; 4, disc with calyx (other floral parts removed), ×6. *E. natalitia*: 5, bisexual flower with front petals and stamens removed, ×6; 6, disc with calyx (other floral parts removed), ×6. (1 from *Renny* 245; 2 from *Van Wyk* 2146; 3 and 4 from *Van Wyk* 2416; 5 and 6 from *Van Wyk* 1119).

SWAZILAND.—2631 (Mbabane): Mbuluzi Falls (–AC), *Compton 25175* (PRE); 4 km NE of Mbabane (–AC), *Kemp 1048* (PRE); c. 1,5 km NW of Mbabane (–AC), *Miller S/138* (PRE); Sibanyone Hill (–CA), *Miller S/264* (PRE).

NATAL.—2632 (Bela Vista): Amanzimnyana, 10 km E of Maputa (–DD), *De Winter & Vahrmeijer 8605* (PRE), near Kosi Bay Nature Reserve (–DD), *Edwards 2553* (PRE), Kosi River (–DD), *Moll & Strey* 3833 (PRE); N bank of Nswamanzi River, near Mhlange Lake (–DD), *Tinley 328* (PRE). 2731 (Louwsburg): Sokosoko Forest (–DC), *Gerstner 4909* (PRE). 2732 (Ubombo): Gwalaweni Forest (–AA), *Botha & Van Wyk 949*; *1122* (PRU); *Vahrmeijer & Hardy 1672* (PRE); Sibayi Dune Forest (–BC) *Sibayi Project 327* (PRE) *Venter 5812* (PRU); Ngoboseleni Lake (–DA), *Ross & Moll 5074* (NH: PRE). 2831 (Nkandla): emGangado (–BB), *Gerstner 5031* (PRE); Eshowe (–CD), *Thode A1237* (NH; PRE). 2832 (Mtubatuba): Mapelan Forest (–AD), *Venter 5573* (PRU); Banghazi Lake (–BA), *Venter 5700* (PRU); Enseleni Nature Reserve near Richards Bay (–CC), *Venter 5913*; *5914*; *6099* (PRU). 2930 (Pietermaritzburg): near Durban (–DD?), *Wood 132* (K; BM; PRE); Westville, Palmiet Nature Reserve (–DD), *Ward 8207* (PRE). 2931 (Stanger): King Hamlyn's Farm, Darnall (–AD), *Moll 3611*; *5503* (NH; PRE). 3030 (Port Shepstone): Isipingo Beach (–BB), *Ward 1000* (PRE).

LOCALITY UNKNOWN.—Cultivated plants on the campus of the University of Pretoria, *Van Wyk 2416*; *2419* (PRU).

Over the whole of its distribution range *E. woodii* shows considerable variation in leaf shape and leaves from more northerly plants are often larger than those from the south. Specimens from open woodland also possess smaller and more coriaceous leaves and tend to be more shrubby than their forest counterparts.

The fruits of *E. woodii* are edible and reported to have a pleasant taste. They are preferred to those of *E. natalitia*, which are less fleshy and have a mealy after-taste.

Common names: iJobe (Sw); umBomvane (Z); 'stawatawane (V). However, some of these names are also recorded for *E. zuluensis* and *E. natalitia*.

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A. E. VAN WYK*

* H. G. W. J. Schweickerdt Herbarium, Department of Botany, University of Pretoria, Pretoria, 0002.

11.3.10 ***Eugenia zeyheri*** (Harv.) Harv. in Gen. S. Afr. Pl.: 99 & 416 (1838). Type: ?Uitenhage, banks of the Vanstaadens River, *Zeyher* 681 (not yet traced).

Myrtus zeyheri Harv. in Gen. S. Afr. Pl.: 99 (1838). Type as above.

Eugenia capensis (Eckl. & Zeyh.) Sond. subsp. *zeyheri* (Harv.) F. White in Kirkia 10(2): 402 (1977). Type as above.

?Eugenia zeyheri (Harv.) Harv. var. *angustifolia* Duemmer in Gdnrs' Chron. ser. 3, 52: 192 (1912). Type: Bathurst Div., at Rietfontein and vicinity, between the Kasuga River and Port Alfred, *Burchell* 3948 (not yet traced).

E. zeyheri is a small tree confined to the eastern Cape and Ciskei. It is particularly common in the districts of Bathurst and Albany. Plants usually grow in patches of relatively dry forest, bush clumps on rocky outcrops or even in valley bushveld. This is the African species of *Eugenia* with the most southerly distribution, and also the native one which ranges well into the Cape Floristic Region (*E. albanensis* may be considered marginal). Although recorded in the forests near Humansdorp, Hankey and Loerie, it does not enter the forests of the Tsitsikama region.

E. zeyheri is characterized by narrowly elliptic to elliptic-lanceolate leaves, flowers with rather short pedicels (2–5 mm long) and an essentially glabrous hypanthium. The leaves are not conspicuously folded upward along the midrib and the primary vein is visible on the upper lamina surface. Sterile specimens may be confused with *E. albanensis* if the growth form is unknown (see 11.3.5).

E. zeyheri var. *angustifolia* is provisionally placed in the synonymy of *E. zeyheri*. Duemmer (1912) described this variety as having leaves 5 mm wide. There is a slight possibility that it could have been based on a collection of *E. albanensis*. Any final decision should be preceded by a thorough study of the type material, which is probably at Kew. *E. zeyheri* is closely related to *E.* sp. A from Natal (see 11.3.12 for a discussion of the diagnostic features).

FIGURE 13, page 226.

REPRESENTATIVE SPECIMENS: *Van Wyk* 3126, 3128, 3131, 3155, 3181, 3182, 3189, 3194, 3213, 3214, 3222, 3232; *Van Wyk & Kok* 5833, 5853 (all in PRU).

11.3.11 ***Eugenia zuluensis*** Duemmer in Gdnrs' Chron. ser. 3, 52: 152 (1912). Type: Zululand, Qudeni Forest, *Davies* 95 ex Herb. *Wood* 8275 (K, holo.!; PRE, iso.!).

Eugenia capensis (Eckl. & Zeyh.) Sond. subsp. *natalitia* (Sond.) F. White in Kirkia 10(2): 402 (1977) pro parte. Type as for *E. natalitia* Sond.

E. zuluensis is a clear-cut species easily distinguished by leaves with the midrib conspicuously raised on the upper lamina surface. The pedicels are relatively long and slender and the flowers nearly always solitary in the axils of leaves or reduced leaves. The mature bole bark is shed in papery flakes (pseudorhytidome), which facilitate the recognition of the species in the forest. It is a species of mist belt forest, often confined to the lower tree stratum. *E. zuluensis* is a very common tree in the understorey of some forests in the southern Natal Midlands, particularly the Wesa Forest System. There are some rare outlier populations of *E. zuluensis* in the escarpment forests of the north-eastern Transvaal, e.g. on Mariepskop and in the Wolkberg–Magoebaskloof area.

Owing to similarities in leaf shape, *E. zuluensis* may be confused with *E. woodii* subsp. *woodii* and *E.* sp. C. Besides the raised midrib by which it is at once distinguished from both these species, *E. zuluensis* does not produce flowers in cymules as in *E. woodii*. *E.* sp. C is usually a canopy tree always confined to coastal forest. Although the bark is also flaky in *E.* sp. C, it does not form a conspicuous pseudorhytidome. Moreover, the phellem usually contains both n- and p-phelloids (only n-phelloids in *E. zuluensis*).

FIGURE 14, page 227.

REPRESENTATIVE SPECIMENS: *Van Wyk* 2153, 2664, 3263, 3264, 3267, 3268, 3291, 3292; *Van Wyk & Venter* 1241, 1242, 1243, 1244, 1249 (all in PRU).

11.3.12 ***Eugenia*** sp. **A**

E. sp. A is a small tree endemic to Natal. Plants usually grow in short, relatively dry shrub forest on outcrops of sandstone. Isolated populations occur from Port Shepstone District in the south to the Pietermaritzburg–Durban area in the north. The species is particularly common in the vegetation covering the slopes of Oribi Gorge in southern Natal. Diagnostic characters include the lanceolate to lanceolate-elliptic leaves with a more or less rounded base and laminas often notably folded upward along the midrib. The primary vein is not clearly visible on the upper lamina surface, but 'overtopped' by adjacent lamina tissue. Leaf arrangement is also very distinctive, particularly in living material. The petioles are appressed to the axis and the laminas strongly ventrally deflexed at the junction with the petioles. This, together with the rather sparse arrangement of the leaves, gives a characteristic appearance to the plants.

E. sp. A is, despite its distinctive vegetative facies, closely related to *E. zeyheri*. The flowers of the two species are fairly similar, although the pedicels tend to be slightly longer [(5)8–15(18) mm] in the former. Specimens referred to as *E. zeyheri* in Van Wyk (1978) are now considered conspecific with *E.* sp. A. A photograph depicting a flowering branchlet of this species appears under the name *E. zeyheri* in Palmer & Pitman (1972, p. 1672). According to the presently proposed new classification of *Eugenia*, 'true' *E. zeyheri* does not occur in Natal but is separated by a marked geographical discontinuity from *E.* sp. A. An alternative approach would be to treat *E.* sp. A as a subspecies of *E. zeyheri*. I have no major objection should the latter course be adopted.

FIGURE 15, page 228.

REPRESENTATIVE SPECIMENS: *Van Wyk* 3269, 3275, 4244, 4513, 4514, 5075, 5078, 5079, 5080, 5082, 5085, 5086; *Van Wyk & Venter* 1291, 1293, 1296 (all in PRU).

11.3.13 ***Eugenia*** sp. **B**

This is a distinctive new species endemic to the sandstone region of southern Natal. It is a small tree from exposed forest margins and bush clumps in the Port Shepstone District. These trees are very common in the forest edges at the upper rim of Oribi Gorge. The species prefers exposed habitats and is rarely encountered in high, sheltered forest. At first glance the thick, leathery leaves on stout, blackish, petioles create the impression that the plants are merely small leaved variants of *E. erythrophylla*. The flowers, however, are quite different from those of the latter species in being distinctly pedicellate with a glabrous hypanthium. Structurally hermaphrodite flowers have the hypanthium globose-obconical compared to the obconical state in *E. erythrophylla*. Perhaps the most noticeable feature of the new species is the dense indumentum of appressed hairs on the very young leaves. The hairs have a silvery sheen and are occasionally an attractive coral pink, giving the impression of a tree profusely flowering. The indumentum on young leaves of *E. erythrophylla* is quite different in being tomentose and without the sheen. It is also more persistent, often still present on fully expanded young leaves.

E. erythrophylla also occurs in southern Natal but has not yet been found sympatrically with *E.* sp. B. In a small relic patch of mutilated forest *ca.* 6 km from Port Shepstone on the road to Harding, *E.* sp. B was recorded growing together with *E. natalitia* and *E.* sp. C. These three species occurred in large numbers and were completely mixed without any indication of habitat segregation. Unfortunately this forest remnant was recently buried under gravel and rock during a road widening operation.

FIGURE 16, page 229.

REPRESENTATIVE SPECIMENS: *Van Wyk* 2344, 2629, 3272, 4183, 4213, 4239, 4240, 4241, 4242, 4339, 4343, 4344; *Van Wyk & Venter* 1276, 1277, 1280, 1302 (all in PRU).

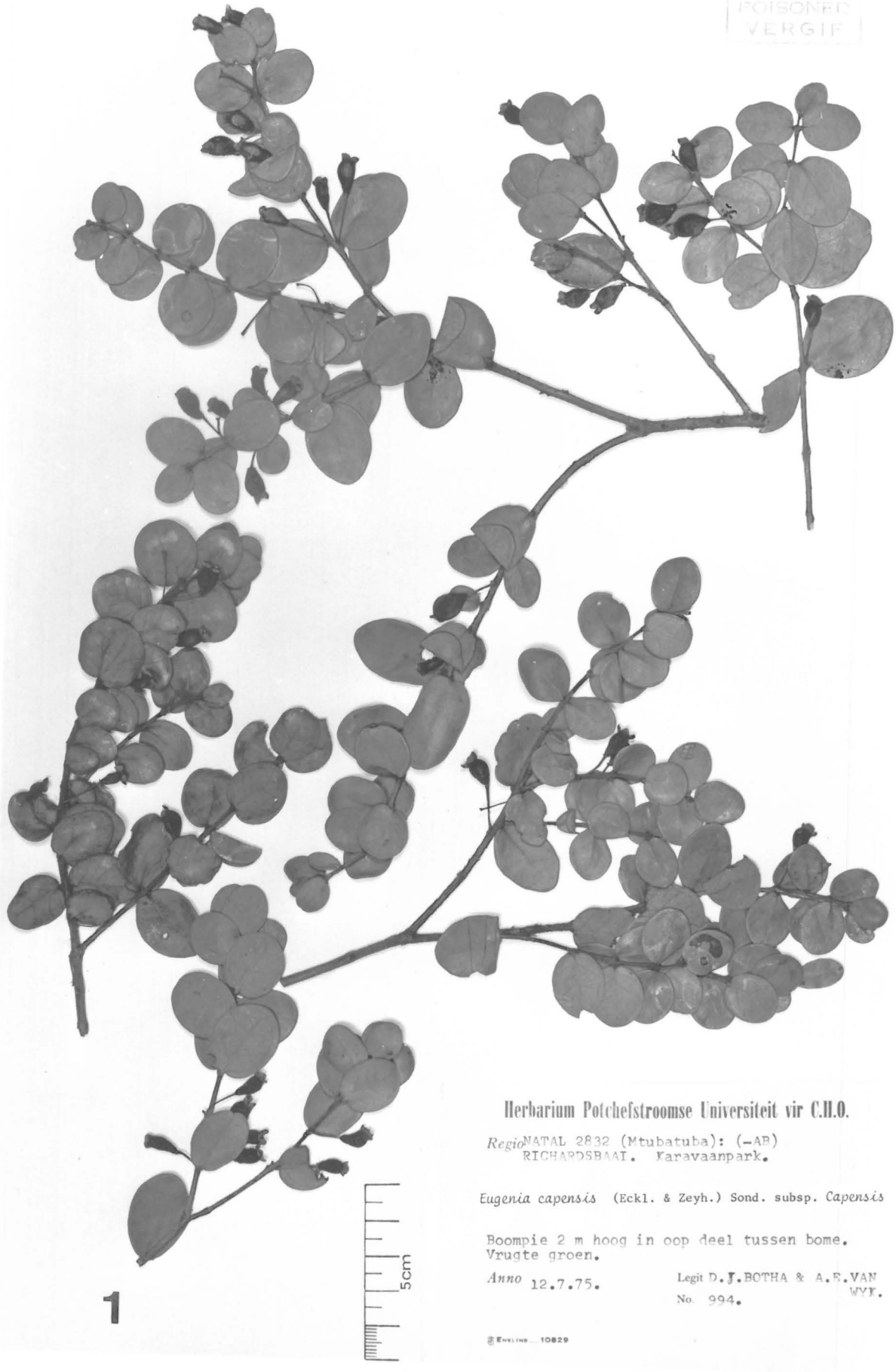
11.3.14 ***Eugenia*** sp. **C**

E. sp. C is a large canopy tree in coastal forest. It is endemic to the sandstone region of southern Natal and Pondoland. The leaves are elliptic-obovate with the apex bluntly acuminate or caudate-acute and the base narrowly cuneate to narrowly attenuate. This may cause confusion with *E. woodii* subsp. *woodii* and *E. zuluensis*, neither of which occurs in the same region as the new species. Perhaps the best way to give a diagnosis of *E.* sp. C is to summarize negative character states. It lacks the cymules, sericeous hypanthium and hairy young leaves of *E. woodii*. It does not have leaves with the midrib conspicuously raised on the upper surface; it is also not a subcanopy tree in mist belt forest such as *E. zuluensis* is. It furthermore lacks some of the distinctive bark features of the latter species (see 11.3.11).

E. sp. C is often associated with *E. natalitia*. A form of *E. natalitia* in forests of the Ntsubane region in Pondoland is so similar in vegetative features to *E.* sp. C, that careful study is required to distinguish between the two taxa. A reliable aid is to determine the position of the first-formed stem periderm in hand-cut sections.

FIGURE 17, page 230.

REPRESENTATIVE SPECIMENS: *Schrire, Van Wyk & Abbott* 1781; *Van Wyk* 1581, 2324, 2343, 3295, 5109, 5115, 5151, 5152, 5389, 6080 (all in PRU).



Herbarium Potchefstroomse Universiteit vir C.H.O.

Regio NATAL 2832 (Mtubatuba): (-AB)
RICHARDSBAAI. Karavaanpark.

Eugenia capensis (Eckl. & Zeyh.) Sond. subsp. *Capensis*

Boompie 2 m hoog in oop deel tussen bome.
Vrugte groen.

Anno 12.7.75. Legit D.J.BOTHA & A.E.VAN WYK.

No. 994.

ENGLING 10829

H.G.W.J. SCHWEICKERDT HERBARIUM (PRU)
UNIVERSITEIT PRETORIA UNIVERSITY

Ruitverw./ Grid. Ref. 3030 CA	Regio
Fort Shepstone	Anno 09/01/82
Legit & No. A.E. van Wyk 5413	Alt

Eugenia capensis (Eckl. & Zeyh.) Sond. subsp. *gueinzii* (Sond.) F.White

Lokaliteit / Locality: Umbi Gorge, Fair Acres.

Habitat: Grasveld.

Grond / Soil	Aspek / Aspect
Vog / Moisture	Helling / Slope

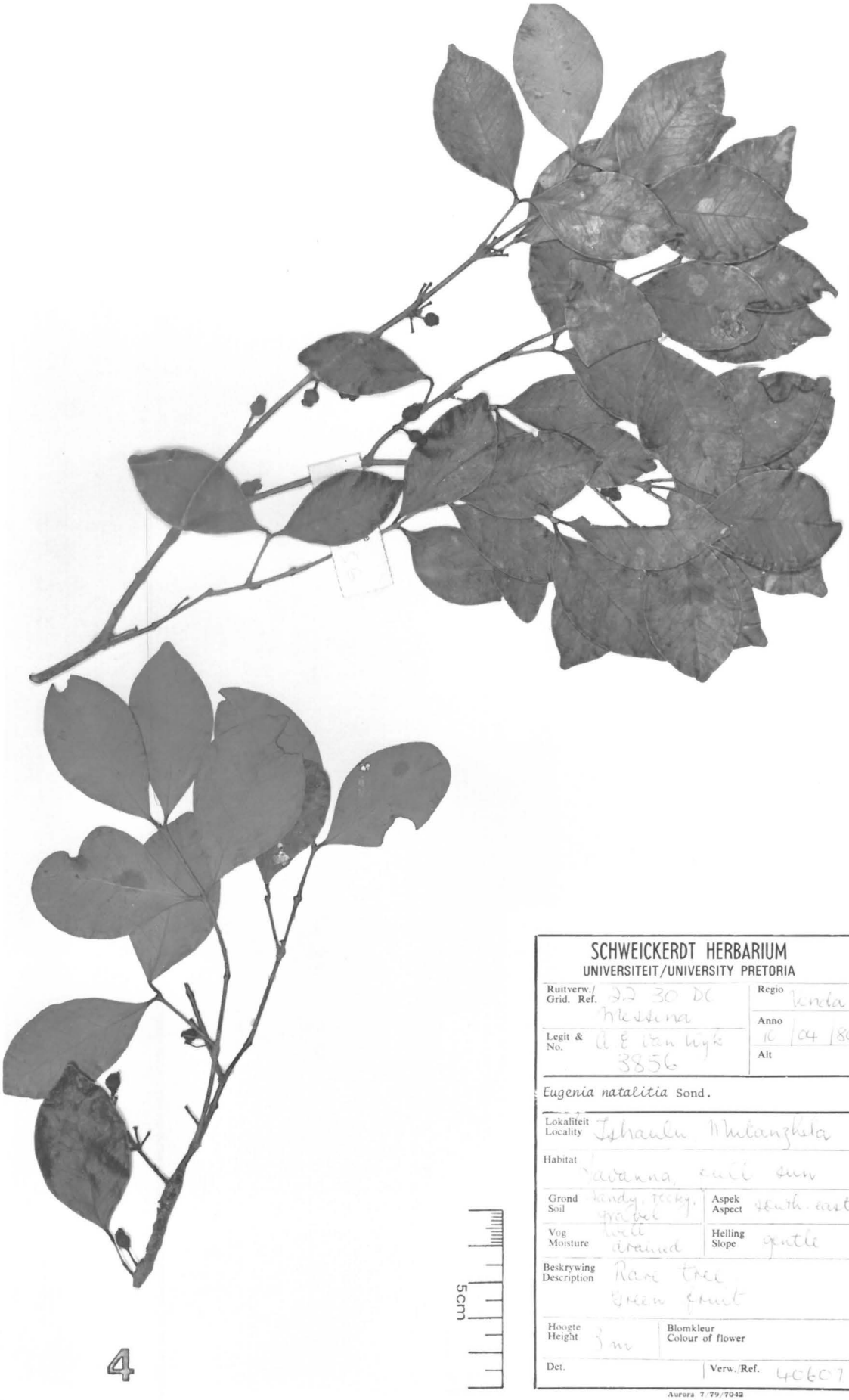
Beskrywing / Description: Halfstruik met blom-knoppe

Hoogte / Height 0,5m	Blomkleur / Colour of flower
Det.	Verw./Ref.

AURORA 5/81/1531

5cm

2



SCHWEICKERDT HERBARIUM
UNIVERSITEIT/UNIVERSITY PRETORIA

Ruitverw./ Grid. Ref. 22 30 DC Messina	Regio Venda
Legit & No. L & Van Wyk 3856	Anno 10 / 04 / 80
	Alt

Eugenia natalitia Sond.

Lokaliteit Locality Tshaulu Mutanzhsta	
Habitat Savanna, cult. dun	
Grond Soil sandy, rocky, gravel	Aspek Aspect south-east
Vog Moisture well drained	Helling Slope gentle
Beskrywing Description Rare tree Green fruit	
Hoogte Height 5 m	Blomkleur Colour of flower
Det.	Verw./Ref. 40607

Aurora 7/79/7042

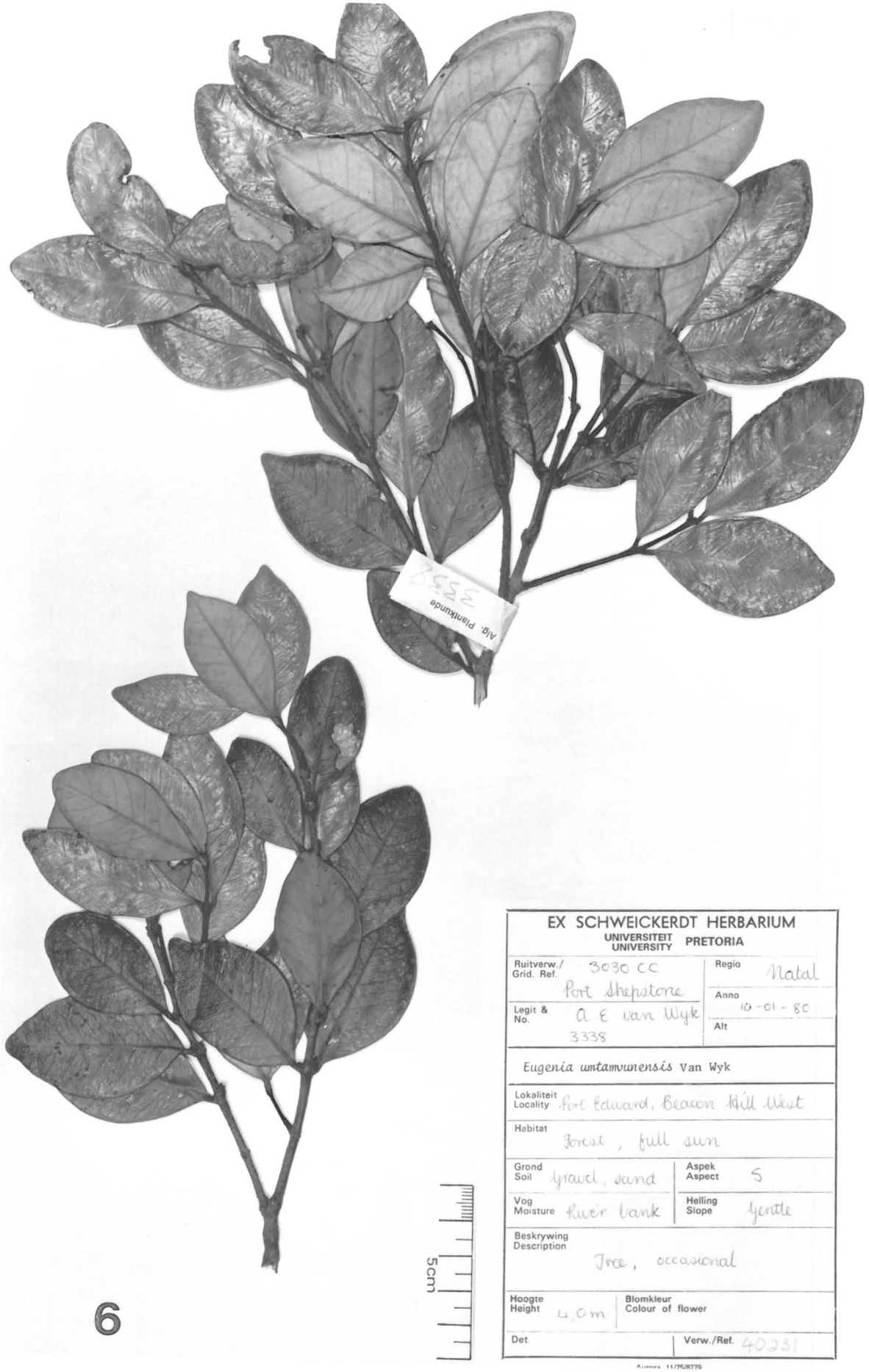
EX SCHWEICKERDT HERBARIUM
UNIVERSITEIT PRETORIA
UNIVERSITY

Ruitverw./ Grid. Ref. 30 30 CA
Regio Pretoria
Anno
Legit & No. 3274
Alt

Eugenia simii Duemmer

Lokaliteit Locality
Habitat
Grond Soil
Aspek Aspect
Vog Moisture
Helling Slope
Beskrywing Description
Hoogte Height
Blomkleur Colour of flower
Det.
Verw./Ref. 40212

Aurora 11/75/8779



EX SCHWEICKERDT HERBARIUM
UNIVERSITEIT PRETORIA
UNIVERSITY

Ruitverw./ Grid. Ref. 3030 CC Port Shepstone	Regio Natal
Legit & No. A E van Wyk 3338	Anno 10-01-80
	Alt

Eugenia umtamvunensis Van Wyk

Lokaliteit / Locality: Port Edward, Beacon Hill West

Habitat: Forest, full sun

Grond / Soil: gravel, sand | Aspek / Aspect: S

Vog / Moisture: River bank | Helling / Slope: gentle

Beskrywing / Description: Tree, occasional

Hoogte / Height: 4,0 m | Blomkleur / Colour of flower:

Det. | Verw./Ref. 4023

POISONED
VERGIF

5cm

7

H.G.W.J. SCHWEICKERDT HERBARIUM (PRU)
UNIVERSITEIT PRETORIA UNIVERSITY

Ruitverw./ Grid. Ref.	Regio
Legit & No.	Anno
	Alt

Eugenia albanensis Sond.

Lokaliteit
Locality

Habitat

Grond Soil	Aspek Aspect
Vog Moisture	Helling Slope

Beskrywing
Description

Hoogte Height	Blomkleur Colour of flower
Det.	Verw./Ref.

AURORA

H.G.W.J. SCHWEICKERDT HERBARIUM (PRU)
UNIVERSITEIT PRETORIA UNIVERSITY

Ruitverw./ Grid. Ref. 3130 AA Port Edward | Regio Natal
Legit & No. A.E. van Wyk 6091 | Anno 03 09 1983 | Alt

Eugenia erythrophylla Strey

Lokaliteit / Locality Umtamvuna - Nature Reserve, Kranz Valley Clearwater
Habitat Woudrand.
Grond / Soil | Aspek / Aspect
Vog / Moisture | Helling / Slope
Beskrywing / Description Boom, volop.
Hoogte / Height 5m | Blomkleur / Colour of flower
Det. | Verw./Ref.

AURORA 6/82/4054

5cm

8

National Herbarium, Pretoria
PRE Neg. No. 6927
5cm
G.P.S. (F-L) LTD (52)

9

NATIONAL HERBARIUM, PRETORIA.

No. — District Ermelo Tvl.
Eugenia pusilla, N.E.Br
/ fide Kew.
att'd
Alt. Date Coll. W. O. Forbes
Collector's No. —
6059—1.9.21—5000
= Govt: Herb. 6350

NATAL
NATALSE HERBARIUM DURBAN

3129 BD Port St. Johns Schrire, van Wyk & Abbott 1816	Grid Ref./ Ruitverw. Legit & No.
Regio Transkei Anno 16.06.1984 Alt.	

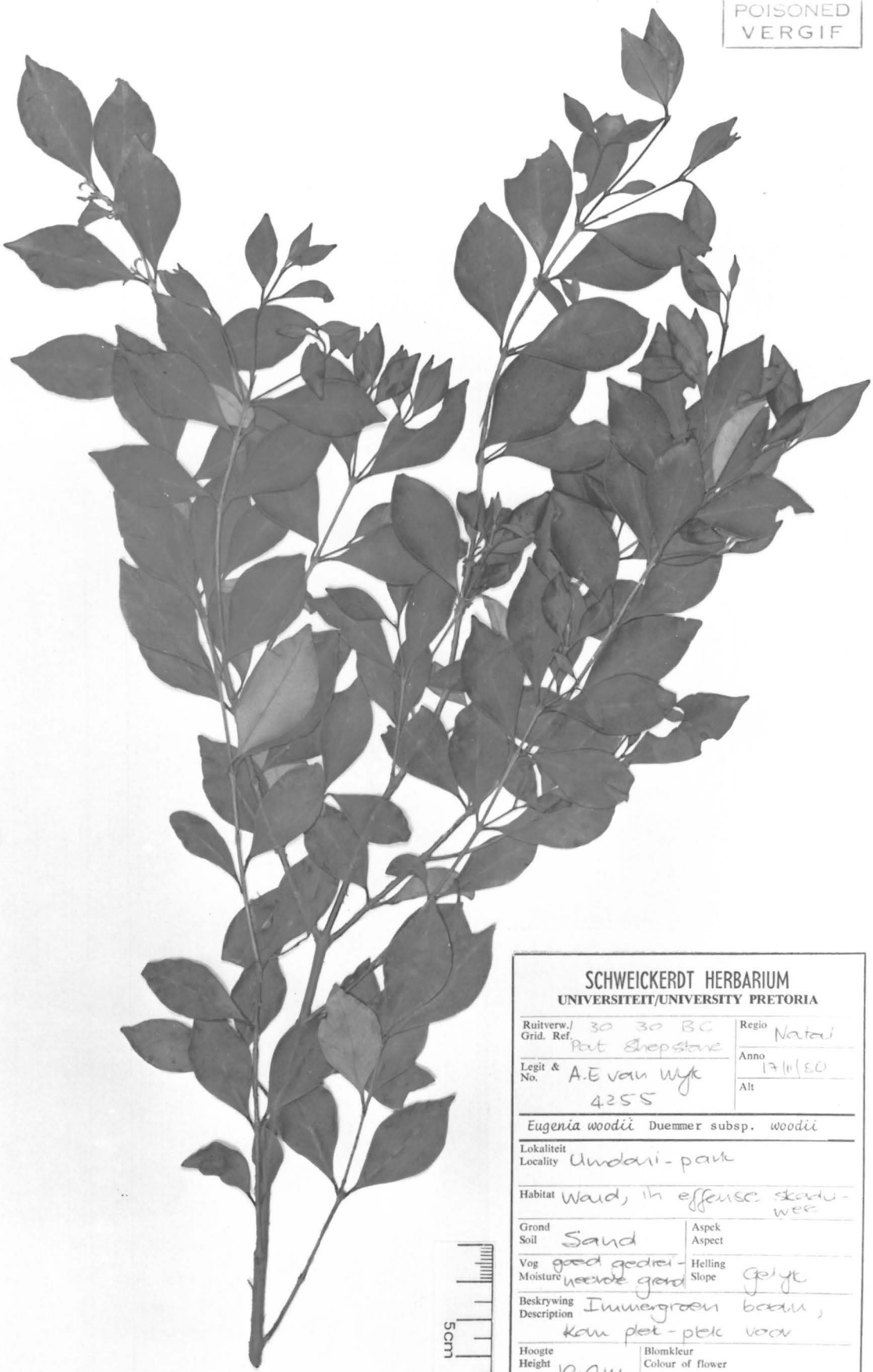
Eugenia verdoorniae Van Wyk

Mkambati Nature Reserve,
Daza River.
Small tree, riverbank.
Flowers White - male.
To 2m high.

Det. | Ref./Verw. 5578

GP-S-(F)-8

POISONED
VERGIF



SCHWEICKERDT HERBARIUM
UNIVERSITEIT/UNIVERSITY PRETORIA

Ruitverw./ Grid. Ref. 30 30 BC Pot Shepstone	Regio Natal
Legit & No. A.E van Wyk 4255	Anno 17/11/80
	Alt

Eugenia woodii Duemmer subsp. *woodii*

Lokaliteit / Locality Umdoni-park

Habitat Woud, in effense skaduwee

Grond / Soil Sand	Aspek / Aspect
Vog / Moisture goed gedreineerde grond	Helling / Slope gelyk

Beskrywing / Description Immergroen bosdier, kan plek-plek voorkom

Hoogte / Height 10,0 m	Blomkleur / Colour of flower
Det.	Verw./Ref.

AURORA 7/80/9511

11

5cm

POISONED
VERGIF

H.G.W.J. SCHWEICKERDT HERBARIUM (PRU)
UNIVERSITEIT PRETORIA UNIVERSITY

Ruitverw./ Grid. Ref. 25 28 CA Pretoria	Regio Transvaal
Legit & No. A.E. van Wyk 5042	Anno 25/10/1981
	Alt

Eugenia woodii Duemmer subsp. A

Lokaliteit / Locality: Pretoria, Universiteit van Pretoria, kampus

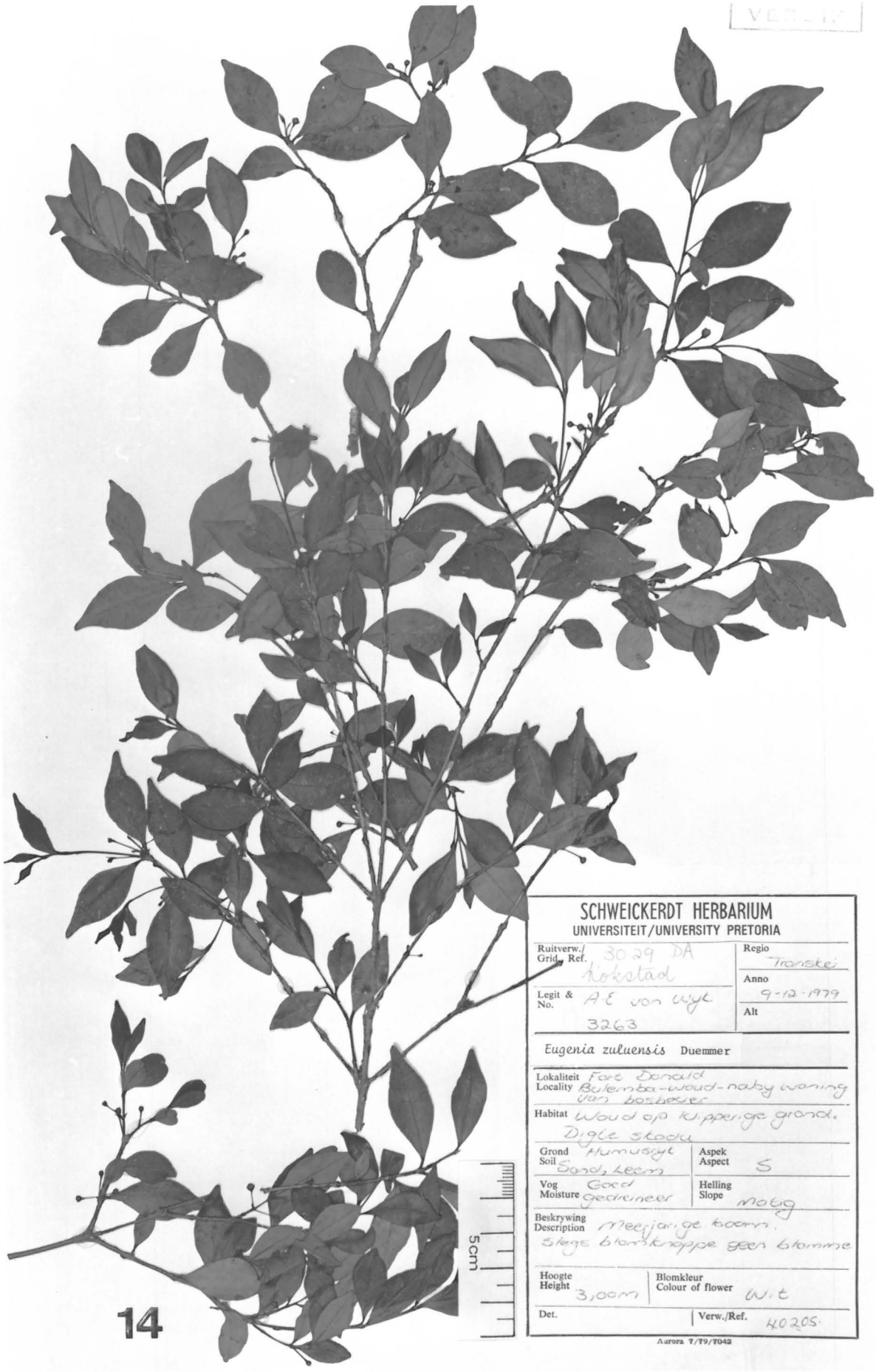
Habitat

Grond / Soil	Aspek / Aspect
Vog / Moisture	Helling / Slope

Beskrywing / Description: Blomme enkel of in kort raseem.

Hoogte / Height	Blomkleur / Colour of flower
Det.	Verw./Ref.

AURORA 5/81/1531



H.G.W.J. SCHWEICKERDT HERBARIUM (PRU)
UNIVERSITEIT PRETORIA UNIVERSITY

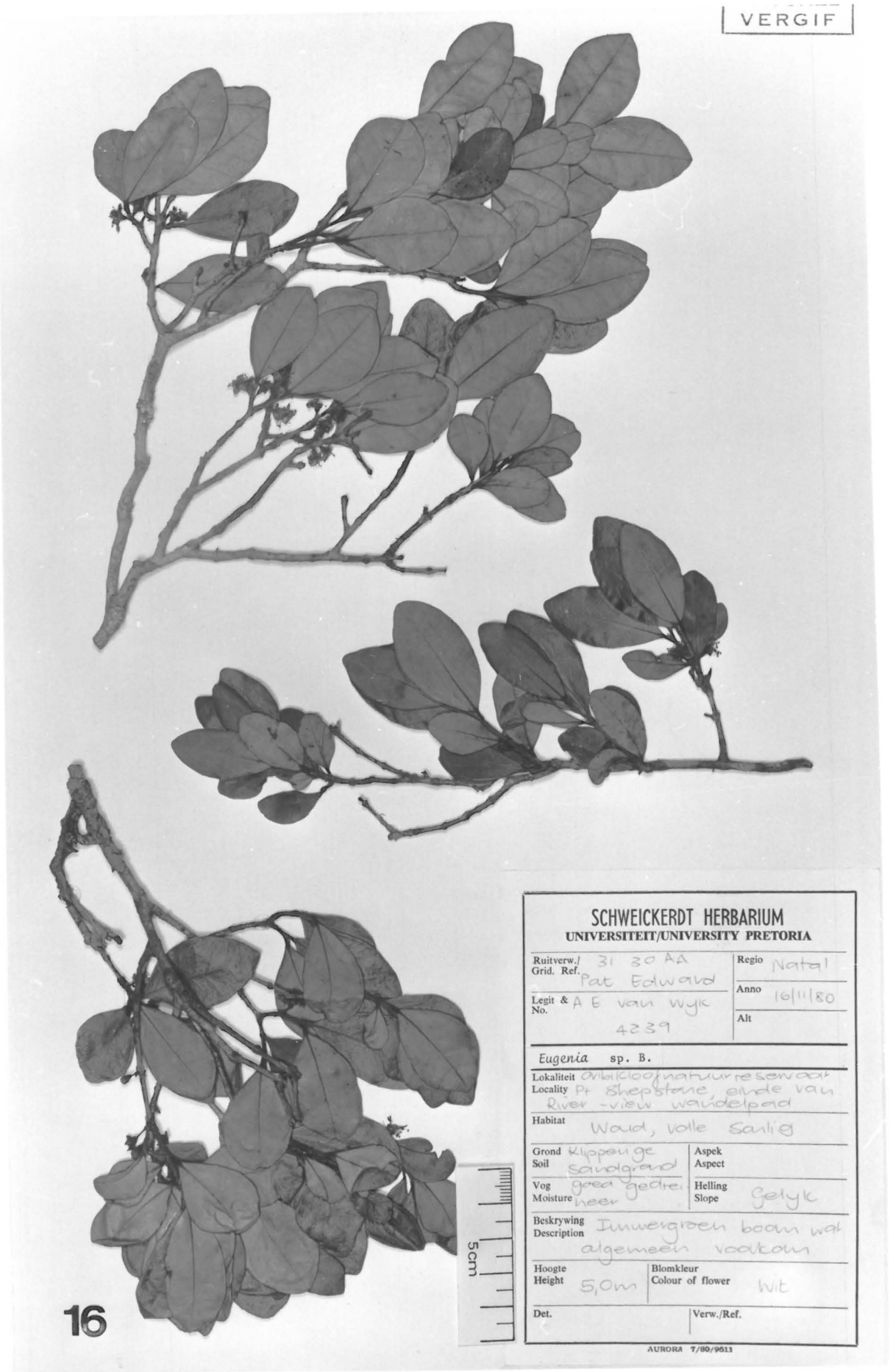
Ruitverw./ Grid. Ref. 30 30 CA Pevt Shepstone
Regio Natal
Legit & No. G.E. van Wyk 5087
Anno 31/10/1981
Alt

Eugenia sp. A.

Lokaliteit / Locality Oribi Gorge Natuurreservaat.
Habitat
Grond / Soil
Aspek / Aspect
Vog / Moisture
Helling / Slope
Beskrywing / Description Boom
Hoogte / Height 2m
Blomkleur / Colour of flower Wit ♀
Det.
Verw./Ref.

AURORA 5/81/1531

VERGIF



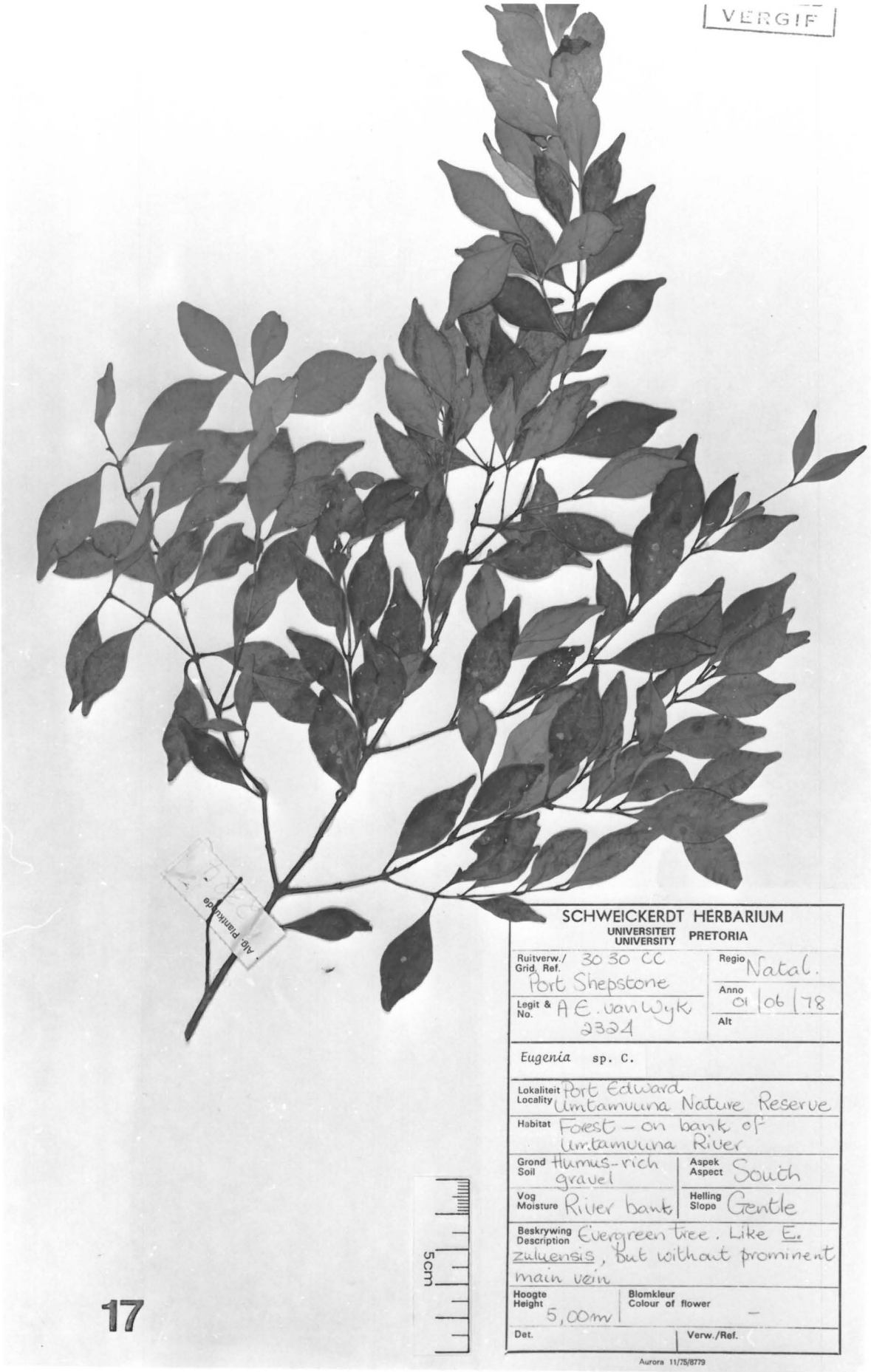
SCHWEICKERDT HERBARIUM
UNIVERSITEIT/UNIVERSITY PRETORIA

Ruitverw./ Grid. Ref. 31 30 AA Pat Edward
Regio Natal
Legit & No. A E van Wyk 4239
Anno 16/11/80
Alt

Eugenia sp. B.

Lokaliteit / Locality Oribi Gloo/natuurreservaat Pt Shepstone, linde van River-view wandelpad
Habitat Woud, volle Sanlig
Grond / Soil Klipperige sandgrond
Aspek / Aspect
Vog / Moisture goed gedreineer
Helling / Slope Gelyk
Beskrywing / Description Immergroen boom wat algemeen voorkom
Hoogte / Height 5,0m
Blomkleur / Colour of flower Wit
Det.
Verw./Ref.

AURORA 7/80/9611



SCHWEICKERDT HERBARIUM
UNIVERSITEIT PRETORIA
UNIVERSITY

Ruitverw./ Grid Ref. 3030 CC Port Shepstone	Regio Natal.
Legit & No. A E. van Wyk 2324	Anno 01/06/78
	Alt

Eugenia sp. C.

Lokaliteit/Locality: Port Edward Umtamvuna Nature Reserve

Habitat: Forest – on bank of Umtamvuna River

Grond/Soil: Humus-rich gravel	Aspek/Aspect: South
Vog/Moisture: River bank	Helling/Slope: Gentle

Beskrywing/Description: Evergreen tree. Like *E. zuluensis*, but without prominent main vein

Hoogte/Height: 5,00m	Blomkleur/Colour of flower: –
Det.	Verw./Ref.

Aurora 11/75/8779

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VAN WYK, A.E. & LOWREY, T.K. 198–. Studies on the reproductive biology of *Eugenia* L. (Myrtaceae) in southern Africa. Proceedings of the 11th AETFAT Congress (in press).

SUMMARY

CONTRIBUTIONS TOWARDS A NEW CLASSIFICATION OF *EUGENIA* L. (MYRTACEAE) IN SOUTHERN AFRICA

by

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This study extends the work on the comparative stem and leaf anatomy of the southern African species of *Eugenia* presented by the author as an M.Sc. thesis in 1978. Additional sources of potential taxonomic evidence were studied in the light of the new taxonomic framework suggested by the anatomical findings. The principal objective was to evaluate the taxonomic significance of various characters as an aid towards a regional revision of this taxonomically difficult genus.

Contributions are presented on reproductive biology, foliar leaf organography, morphology and ontogeny of the seed and the structure of the stomata, wood, bark and pollen. The thesis is a compilation of 12 papers published in scientific journals over a period of about seven years. It also contains a synthesis of the principal findings, an outline of a proposed new classification of *Eugenia* in southern Africa with keys to the principal taxa, supplemented by notes on diagnostic characters, synonymy, typification and geographical distribution.

Anatomical and morphological data from different sources (especially the first-formed stem periderm, bark, stomata, inflorescences, seeds and fruits) provide convincing evidence that *Eugenia* in southern Africa constitutes a heterogeneous assemblage of two co-ordinate groups of species. Group X seems to be most closely related to the mainly New World species of *Eugenia*, whereas group Y relates to the Old World genus *Jossinia* DC. (usually reduced to the synonymy of *Eugenia*). Owing to the lack of comparative data on *Eugenia* elsewhere, both supraspecific groups are provisionally maintained as informal categories.

The present study has rendered untenable the inclusive specific circumscriptions recently proposed for *Eugenia* in southern Africa. In a new classification, 14 species (five new) and five subspecies are proposed for the FSA region, compared to two species and at least six subspecies maintained by White (1977 & 1978). New taxa lacking valid names are provisionally referred to by alphabetical characters. Group X consists of *E. capensis* (Eckl. & Zeyh.) Sond. with subspp. *capensis, gueinzii* (Sond.) F. White and A [probably within the concept of subsp. *aschersoniana* (F. Hoffm.) F. White], *E. natalitia* Sond., *E. simii* Duemmer and *E. umtamvunensis* Van Wyk. Group Y includes *E. albanensis* Sond., *E. erythrophylla* Strey, *E. pusilla* N.E. Br., *E. verdoorniae* Van Wyk, *E. woodii* Duemmer with subspp. *woodii* and A, *E. zeyheri* (Harv.) Harv., *E. zuluensis* Duemmer and *Eugenia* spp. A, B and C. Species diagnoses are mainly based on habit, habitat, geographical distribution, bark structure, foliar leaf organography, type of indumentum, inflorescence structure and floral morphology—particularly the stigma and hypanthium in structural hermaphrodites.

Noteworthy findings include the presence of water-stomata, conspicuous lipid bodies in the subsidiary cells, wood with pith flecks (pathological) and prismatic crystals enclosed by a thick lignified sheath, bark with a pseudocortex in group X and two types of phelloid cells. A new term 'anomostaurocytic' is proposed for the stomatal type in the native species. For the first time pollen dimorphism and a pachychalazal seed coat are reported for members of the Myrtaceae. *Eugenia* in southern Africa displays morphological androdioecy but is functionally dioecious.

OPSOMMING

BYDRAES TOT 'N NUWE KLASSIFIKASIE VIR *EUGENIA* L. (MYRTACEAE) IN SUIDER-AFRIKA

deur

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Die huidige ondersoek is 'n voortsetting van die vergelykende stingel- en blaaranatomiese werk op die Suider-Afrikaanse *Eugenia*-spesies wat in 1978 as 'n M.Sc.-verhandeling voorgelê is. Bykomende bronne van potensiële taksonomiese getuienis is ondersoek in die lig van die nuwe taksonomiese raamwerk wat deur die anatomiese bevindings daargestel is. Die hoofdoelwit was die evaluering van die taksonomiese belangrikheid van verskillende kenmerke as hulpmiddels in 'n plaaslike hersiening van hierdie taksonomies-moelike genus.

Bydraes oor veral die voortplantingsbiologie, loofblaarorganografie, saadmorfologie en -ontogenie en struktuur van die stomas, hout, bas en stuifmeel word verskaf. Die proefskrif is uit 12 artikels wat oor 'n tydperk van omtrent sewe jaar in wetenskaplike tydskrifte gepubliseer is, saamgestel. Dit bevat ook 'n sintese van die belangrikste bevindings, die raamwerk van 'n voorgestelde nuwe klassifikasie van *Eugenia* in Suider-Afrika met sleutels tot die belangrikste taksons, aangevul deur aantekeninge oor diagnostiese kenmerke, sinonimie, tipifisering en geografiese verspreiding.

Anatomiese en morfologiese gegewens van verskillende bronne (veral die eerste-gevormde stingelperiderm, bas, stomas, bloeiwyses, saad en vrugte) verskaf oortuigende getuienis dat *Eugenia* in Suider-Afrika 'n heterogene groepering is wat uit twee gelykwaardige spesiegroepe bestaan. Spesiegroep X is skynbaar die naaste verwant aan die *Eugenia*-spesies van hoofsaaklik die Nuwe Wêreld, terwyl groep Y verwantskap met *Jossinia* DC. (gewoonlik as 'n sinoniem van *Eugenia* beskou) in die Ou Wêreld vertoon. Weens die gebrek aan vergelykende inligting oor *Eugenia* in ander wêrelddele, word beide supraspesifieke groepe voorlopig as informele kategorieë gehandhaaf.

Die huidige ondersoek maak die omvattende spesie-omgrensings wat onlangs vir *Eugenia* in Suider-Afrika voorgestel is, onaanvaarbaar. In 'n nuwe klassifikasie word 14 spesies (vyf nuut) en vyf subspesies vir die FSA-gebied voorgestel, teenoor die twee spesies en minstens ses subspesies wat White (1977 & 1978) onderskei. Letters van die alfabet word voorlopig gebruik om na nuwe taksons sonder geldige name te verwys. Groep X bestaan uit *E. capensis* (Eckl. & Zeyh.) Sond. met subspp. *capensis, gueinzii* (Sond.) F. White en A [moontlik binne die konsep van subsp. *aschersoniana* (F. Hoffm.) F. White], *E. natalitia* Sond., *E. simii* Duemmer en *E. umtamvunensis* Van Wyk. Groep Y sluit in *E. albanensis* Sond., *E. erythrophylla* Strey, *E. pusilla* N.E. Br., *E. verdoorniae* Van Wyk, *E. woodii* Duemmer met subspp. *woodii* en A, *E. zeyheri* (Harv.) Harv., *E. zuluensis* Duemmer en *Eugenia* spp. A, B en C. Spesiediagnoses is hoofsaaklik gebaseer op groeivorm, habitat, geografiese verspreiding, basstruktuur, loofblaarorganografie, indumentum-tipe, bloeiwysestruktuur en blommorfologie—veral die stempel en hipantium van strukturele hermafrodiete.

Vermeldingswaardige bevindings sluit in die aanwesigheid van waterstomas, opvallende lipiedliggame in die hulpselle, hout met murgvlekke (patologies) en prismatiese kristalle omsluit deur 'n gelignifiseerde skede, bas met 'n pseudokorteks by groep X en twee tipes felloïedselle. Die nuwe term 'anomostaurosities' word vir die stomatipe van die inheemse spesies voorgestel. Stuifmeeldimorfisme en 'n pagichalasale saadhuid is vir die eerste keer by verteenwoordigers van die Myrtaceae aangeteken. *Eugenia* in Suider-Afrika vertoon morfologiese andresie maar is eintlik funksioneel tweehuisig.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to the many persons and institutions who have offered encouragement, assistance and co-operation in the preparation of this thesis, namely:

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It is a pleasure to acknowledge the close co-operation from the following people in papers incorporated in this thesis: Profs. D.J. Botha and J. Coetzee (first-formed stem periderm), Mrs. R. Botha (seed ontogeny), Miss I. Dedekind (pollen morphology), Dr. T.K. Lowrey (reproductive biology) and Mr. S.G. Menezes (wood anatomy).

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CURRICULUM VITAE

Abraham Erasmus van Wyk was born on 19 February 1952 in Wolmaransstad. He attended the Wolmaransstadse Hoërskool where he matriculated in 1969. During 1970 he did his military training at the Army Gymnasium in Heidelberg, Tvl. In 1971 he enrolled at the Potchefstroom University for C.H.E., and in 1973 was awarded a B.Sc. degree with distinctions in Botany, Human Physiology and Zoology. This was followed by a B.Sc. (Hons.) in Botany in 1974 and an M.Sc. in 1977, both with distinction. Through part-time study he obtained a Diploma in Higher Education (with distinction) from the same University in 1976.

From 1974–1976 he was appointed in various capacities at the Department of Botany, Potchefstroom University for C.H.E. In 1977 he joined the lecturing staff of the Department of Botany, University of Pretoria. Furthermore he has been engaged mainly in systematic anatomical research and has collected plant specimens from all over southern Africa. His interest in particularly woody plants has led to the discovery and description of a number of new species. Mr. Van Wyk has presented papers at congresses both locally and abroad. He is the author or co-author of about 30 scientific and popular scientific papers.

LIST OF PUBLISHED PAPERS

1978

1. VAN WYK, A.E. 1978. *Syzygium pondoense* (Myrtaceae) rediscovered. *Bothalia* 12: 449–451.

1979

2. VAN WYK, A.E. 1979. A new species of *Eugenia* L. (Myrtaceae) from southern Natal and Transkei. *Jl S. Afr. Bot.* 45: 273–277.

1980

3. NETSHIUNGANI, E.N. & VAN WYK, A.E. 1980. Mutavhatsindi: Mysterious plant from Venda. *Veld & Flora* 66: 87–90.
4. VAN WYK, A.E. 1980. The identity of *Eugenia woodii*. In: Notes on African Plants: Myrtaceae. *Bothalia* 13: 142–145.
5. VAN WYK, A.E. 1980. A note on the seed morphology of the genus *Eugenia* L. (Myrtaceae) in southern Africa. *Jl S. Afr. Bot.* 46: 115–119.
6. VAN WYK, A.E., BOTHA, D.J. & COETZEE, J. 1980. The genus *Eugenia* L. (Myrtaceae) in southern Africa. I. The nature and taxonomic value of the first-formed stem periderm. *Jl S. Afr. Bot.* 46: 67–88.

1981

7. NETSHIUNGANI, E.N., VAN WYK, A.E. & LINGER, M.T. 1981. Thathe, Holy forest of the Vhavenda. *Veld & Flora* 67: 51–52.
8. VAN WYK, A.E. 1981. Vir 'n groter Umtamvuna-natuurreservaat. *Dendrologiese Tydskrif* 1: 106–108.
9. VAN WYK, A.E. & CLAASSEN, M.I. 1981. Sex reversal in *Encephalartos umbeluziensis*. *Veld & Flora* 67: 120–122.

1982

10. DU PLESSIS, E. & VAN WYK, A.E. 1982. The genus *Eugenia* (Myrtaceae) in southern Africa. Taxometrics of foliar organography. *S. Afr. J. Bot.* 1: 147–157.
11. VAN WYK, A.E. 1982. Seldsame bome – Verspreidingsfaktore. *Dendrologiese Tydskrif* 2 (1 & 2): 3–24.
12. VAN WYK, A.E. 1982. A new species of *Eugenia* L. (Myrtaceae) from southern Natal. *S. Afr. J. Bot.* 1: 158–163.
13. VAN WYK, A.E., IMMELMAN, K. & DE VILLIERS, P.D. 1982. Southern African Malpighiaceae : unexplored horticultural potential. *Veld & Flora* 68: 75–77.
14. VAN WYK, A.E. & LÖTTER, L.A. 1982. *Manilkara nicholsonii* (Sapotaceae), a new species from southern Natal. *S. Afr. J. Bot.* 1: 33–37.
15. VAN WYK, A.E., ROBBERTSE, P.J. & KOK, P.D.F. 1982. The genus *Eugenia* L. (Myrtaceae) in southern Africa. The structure and taxonomic value of stomata. *Bot. J. Linn. Soc.* 84: 41–56.

1983

16. ROBBERTSE, P.J. & VAN WYK, A.E. 1983. Inheemse bome vir die tuin: Witstinkhout (*Celtis africana*). *Tukkiewerf* 9(1): 27.
17. ROBBERTSE, P.J. & VAN WYK, A.E. 1983. Inheemse bome vir die tuin: Bome met mooi herfskleure. *Tukkiewerf* 9(2): 21–22.
18. VAN WYK, A.E. 1983. A new species of *Rinorea* (Violaceae) from southern Natal and northern Transkei. *S. Afr. J. Bot.* 2: 168–172.
19. VAN WYK, A.E. 1983. The correct name for *Memecylon grandiflorum* (Melastomataceae). *S. Afr. J. Bot.* 2: 173.
20. VAN WYK, A.E., ROBBERTSE, P.J. & KOK, P.D.F. 1983. The genus *Eugenia* (Myrtaceae) in southern Africa: Structure and taxonomic value of wood. *S. Afr. J. Bot.* 2: 135–151.

1984

21. THERON, G.K., VAN ROOYEN, N., VAN ROOYEN, M.W., VAN WYK, A.E. & JANSE VAN RENSBURG, D. 1984. Die bome van die laer Kuisebrivier, Suidwes-Afrika/Namibië. *Dendrologiese Tydskrif* 4: 3–20.
22. VAN WYK, A.E. 1984. A new species of *Maytenus* (Celastraceae) from southern Natal. *S. Afr. J. Bot.* 3: 115–119.
23. VAN WYK, A.E. 1984. A new species of *Combretum* from Venda and taxonomic notes on the section *Angustimarginata* (Combretaceae). *S. Afr. J. Bot.* 3: 125–134.
24. VAN WYK, A.E. & BOTHA, R. 1984. The genus *Eugenia* (Myrtaceae) in southern Africa : Ontogeny and taxonomic value of the seed. *S. Afr. J. Bot.* 3: 63–80.

1985

25. VAN ROOYEN, N. & VAN WYK, A.E. Inheemse bome vir die tuin : Koraalbome. *Tukkiewerf* 11(3): 28–29.
26. VAN ROOYEN, N. & VAN WYK, A.E. 1985. Eenslagtigheid en parasitisme by the suurpruim (*Ximenia caffra* var. *caffra*)/Hosts of sourplum not yet known. *Custos* 14: 19–23.
27. VAN WYK, A.E. 1985. Die vlakappel : 'n vergete veldvrug. *Veld & Flora* 71: 18–21.
28. VAN WYK, A.E. 1985. The genus *Eugenia* (Myrtaceae) in southern Africa : structure and taxonomic value of bark. *S. Afr. J. Bot.* 51: 157–180.
29. VAN WYK, A.E. & DEDEKIND, I. 1985. The genus *Eugenia* (Myrtaceae) in southern Africa : morphology and taxonomic value of pollen. *S. Afr. J. Bot.* 51: 371–378.

SUBMITTED FOR PUBLICATION

30. DAHLGREN, R.M.T. & VAN WYK, A.E. Structures and relationships of families and isolated genera endemic mainly to southern Africa. Proceedings of the 11th AETFAT Plenary Meeting (in press).
31. DU PLESSIS, E. & VAN WYK, A.E. Achariaceae. In: Anatomy of the Dicotyledons, 2nd ed., Eds. Metcalfe, C.R. & Chalk, L. (in preparation).
32. VAN WYK, A.E. & LOWREY, T.K. Studies on the reproductive biology of *Eugenia* L. (Myrtaceae) in southern Africa. Proceedings of the 11th AETFAT Plenary Meeting (in press).

APPENDIX

CORRECTIONS AND ADDITIONAL NOTES

The errors listed below have been corrected on the reprints included in this thesis. They are recorded here for the attention of workers who want to consult the published versions of these papers. Page numbers are those of the original publications. Corrections and notes are supplied separately for each paper. The papers are listed under the heading of the chapter in which they appear in this thesis.

CHAPTER 2

VAN WYK, A.E., ROBBERTSE, P.J. & KOK, P.D.F. 1982. The genus *Eugenia* L. (Myrtaceae) in southern Africa: the structure and taxonomic value of stomata. *Bot. J. Linn. Soc.* 84: 41–56.

CORRECTIONS

p. 54, para. 3, line 8: 'adopted', not 'adapted'
p. 55, para. 1, line 13: '*Forbes s.n. sub PRE 6350 (PRE)*', not '*Forbes 6350 (PRE)*'

NOTES

Patel (1979) proposed a new morphological classification of stomatal complexes. This classification is open to accommodate new types of stomatal complexes, including the stomatal type in the southern African species of *Eugenia*. Hence the regular stomata in the native species can be classified as tri-, tetra- or penta-monocyclic and the water stomata as actino-multi-monocyclic. Note that the stomata surrounded by three subsidiary cells are not aniso-tri-monocyclic, because the size of the subsidiaries does not show the anisocytic pattern. Rasmussen (1981) reviewed, and attempted to rationalize, the terminology for classifying stomata according to their ontogeny. Stomatal development in the southern African species of *Eugenia* is, however, still unknown.

The subsidiary cells in *E. verdoorniae* have now been studied with the transmission electron microscope (unpublished data). No *distinct* membrane surrounds the large lipid bodies present in these cells (see pp. 45 & 53). The lipid bodies are therefore best referred to as lipid (oil) droplets. It is clear that they are not elaioplasts.

CHAPTER 3

DU PLESSIS, E. & VAN WYK, A.E. 1982. The genus *Eugenia* (Myrtaceae) in southern Africa : Taxometrics of foliar organography. *S. Afr. J. Bot.* 1: 147–157.

NOTES

The fact that the results of this study do not reflect the two supraspecific groups among native species of *Eugenia*, could have been influenced by the exclusion of the following two supportive leaf properties (not to mention some additional properties from internal structure). The cuticular membrane in species group X usually shows conspicuous striations but is more or less smooth-surfaced in group Y (Van Wyk 1978; Van Wyk *et al.* 1982). In species group X the lower lamina surface in fresh leaves is usually light green and conspicuously gland-dotted, whereas in group Y it is usually whitish-green and sparingly or obscurely gland-dotted (numerous secretory cavities are nevertheless present in the mesophyll of both groups).

The complete data base employed in this study is supplied in Table 1.

As a matter of interest the revision of Myrtaceae by Berg (1857–59) in Flora Brasiliensis deserves citation. Supplementing the revision are photographs of cleared leaves for many neotropical members of the Myrtoideae.

CHAPTER 4

4.1 VAN WYK, A.E. 1980. A note on the seed morphology of the genus *Eugenia* L. (Myrtaceae) in southern Africa. *Jl S. Afr. Bot.* 46: 115–119.

CORRECTIONS

p. 117, para. 1, line 1: 'darkly coloured', not 'lighter-coloured'
p. 117, para. 2, line 3: 'thicker', not 'thinner'

4.2 VAN WYK, A.E. & BOTHA, R. 1984. The genus *Eugenia* (Myrtaceae) in southern Africa : Ontogeny and taxonomic value of the seed. *S. Afr. J. Bot.* 3: 63–80.

CORRECTIONS

p. 74, caption for Figures 31 & 32, line 2: 'PAS-TB', not 'PAS-TP'
p. 77, right column, para 4, line 6: *'Myrciariopsis'*, not *'Myrcariopsis'*
p. 79, right column, ref. 19: 'DüMMER, R.A.', not 'DüMMER, R.D.'

NOTES

I am now more convinced than before that the seed-coat in seed type Y is pachychalazal. I am also of the opinion that the seed-coat in seed type X is partly derived from chalazal tissue. In seed type X the tissues forming the more darkly coloured areolae visible on the inner surface of the seed-coat are considered homologous to the chalaza-derived parts of the seed-coat in seed type Y. The taxonomic implications of such an interpretation are shortly outlined in Chapter 10 under 10.2. Provisional notes on the seed structure of species of *Eugenia* from the New World and other parts of the Old World are also presented in the latter section.

CHAPTER 5

VAN WYK, A.E., ROBBERTSE, P.J. & KOK, P.D.F. 1983. The genus *Eugenia* (Myrtaceae) in southern Africa : Structure and taxonomic value of wood. *S. Afr. J. Bot.* 2: 135–151.

CORRECTIONS

p. 149, left column, para. 2, line 3: 'androdioecious', not 'andromonoecious'
p. 149, left column, para. 2, line 4: 'andromonoecious', not 'androdioecious'
p. 150, left column, ref. 23: 'DüMMER, R.A.', not 'DüMMER, R.D.'
p. 150, right column, ref. 3: '. . .samples prepared for. . .', not '. . .samples for. . .'
p. 150, right column, ref. 10: 'Observation', not 'Observations'

TABLE 1.— BASIC DATA MATRIX FOR FOLIAR ORGANOGRAPHIC PROPERTIES

PROPERTIES \ OTU's	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1	2,45	3,81	1,48	2,00	2,12	3,22	3,88	5,10	4,74	4,24	3,12	2,22	2,75	3,47	3,28	2,38	1,79	2,54	3,90	2,23	3,34	2,66	3,44	3,14	3,76	2,53	2,62	3,06	4,60	2,55	3,99
2	1,83	2,92	1,02	1,18	1,58	1,88	1,58	2,59	2,26	2,05	1,15	1,00	1,10	1,27	0,75	0,41	0,45	0,27	0,68	0,44	1,23	1,15	1,58	1,46	1,27	1,44	0,94	1,44	2,49	0,86	1,74
3	1,35	1,30	1,45	1,71	1,35	1,71	2,48	1,98	2,10	2,08	2,72	2,23	2,50	2,74	4,39	5,84	4,02	9,47	5,76	5,08	2,73	2,36	2,19	2,16	2,95	1,76	2,80	2,13	1,86	2,96	2,30
4	44,09	45,10	49,57	50,11	44,47	52,57	53,85	50,22	55,38	58,34	59,15	55,15	57,10	60,18	64,16	61,15	60,50	63,30	58,67	65,50	48,08	50,80	50,80	53,89	49,22	53,87	57,18	54,98	52,60	56,22	53,64
5	85,13	84,91	91,95	88,91	85,40	92,36	93,61	91,92	93,06	92,03	98,17	98,97	98,62	97,72	99,32	99,03	98,46	98,46	99,37	97,74	99,33	99,17	98,94	97,52	98,10	97,74	97,94	98,82	98,80	98,08	98,14
6	56,73	56,98	58,38	60,99	57,11	58,87	66,70	61,23	63,52	62,11	65,33	64,05	64,24	64,59	72,09	77,82	72,41	83,77	76,34	74,46	63,59	62,38	60,14	60,09	66,14	58,82	67,57	64,00	59,73	68,52	63,61
7	209,6	238,8	185,4	184,8	212,8	101,4	98,4	114,0	115,8	79,4	66,6	109,2	68.4	57,0	38,4	93,2	77,5	93,9	31,8	53,5	57,6	80,0	61,0	55,8	66,6	123,8	114,6	128,8	133,8	139,0	93,8
8	160,4	161,4	154,2	145,0	154,2	146,8	142,4	117,0	141,8	143,8	102,8	132,0	105,8	90,2	93,8	104,9	133,0	118,0	98,2	121,6	69,4	78,6	70,4	76,4	52,2	97,4	119,4	125,8	94,4	127,4	106,4
9	-1,91	-4,13	-0,34	-0,30	-2,12	5,10	3,60	3,37	3,06	5,86	5,70	3,12	6,20	7,11	7,49	1,95	3,68	1,72	6,48	4,71	7,04	5,51	8,03	9,04	5,22	3,12	2,40	2,33	2,26	1,37	4,07
10	1,24	1,21	1,56	1,83	1,64	1,62	1,32	3,11	1,68	1,50	3,01	2,00	3,12	3,64	2,46	1,68	1,23	0,82	1,65	1,29	6,02	5,29	6,65	5,87	7,11	4,88	2,06	2,25	4,93	1,98	3,26
11	7,2	7,2	7,6	9,2	9,0	10,2	10,6	9,4	10,8	10,2	14,2	10,4	12,0	15,8	15,8	10,8	10,6	11,0	9,2	10,2	13,2	14,6	16,8	13,8	17,6	8,8	11,4	11,0	10,6	11,0	13,6
12	10,00	16,33	10,22	2,50	12,21	5,64	29,03	41,39	52,22	60,39	3,64	4,44	1,43	10,45	24,09	61,43	14,52	16,71	8,72	14,60	46,16	11,14	4,44	31,39	17,51	25,93	36,95	10,98	42,92	21,09	39,90
13	1,80	2,39	2,18	2,49	3,68	2,64	1,58	1,55	1,54	1,89	1,52	1,30	1,45	1,52	1,17	0,80	0,74	0,40	0,56	0,57	1,65	1,74	3,09	2,27	2,09	1,47	1,32	1,66	1,85	1,17	2,08
14	64,0	74,9	54,3	64,1	84,6	58,1	40,9	45,2	48,0	38,2	51,4	48,0	59,5	44,8	55,7	21,2	25,2	44,4	35,5	35,5	50,1	46,1	51,4	46,1	40,0	41,4	52,2	58,3	47,7	37,8	47,8
15	65,15	66,61	59,77	58,80	66,79	60,61	47,08	49,33	53,87	45,90	59,88	60,68	61,71	54,45	61,63	65,59	64,08	69,25	65,31	68,26	65,76	65,87	62,34	63,58	59,28	57,65	64,98	65,52	55,20	55,38	62,47
16	64,53	62,64	57,10	58,60	63,14	58,39	46,96	50,77	53,76	51,50	56,35	61,61	59,69	55,14	54,44	68,92	72,84	81,41	78,44	73,88	67,09	67,10	68,94	65,99	62,44	51,57	61,28	59,64	50,06	54,66	62,22
17	20,13	17,43	17,41	17,13	12,97	15,02	13,08	11,92	15,14	15,20	13,81	11,91	14,16	13,18	13,20	22,98	18,04	19,18	20,50	21,01	10,41	11,22	9,86	10,61	9,09	12,22	13,12	8,57	8,71	12,46	13,82
18	6,7	6,9	9,2	8,3	11,5	12,0	14,3	16,0	14,6	13,1	13,0	13,9	9,5	9,8	17,9	11,4	12,2	7,8	7,3	10,6	13,6	9,0	11,1	10,6	12,6	12,1	16,3	15,9	14,6	17,9	20,8
19	X	X	X	X	X	X	X	X	X	X	X	Y	X	X	X	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
20	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	1	1	1	1	1	1

OTU's: 1–5 : *E. capensis*
6–10 : *E.* cf. *mossambicensis*
11,13–15 : *E. simii*
16–20 : *E. verdoorniae*
21–25 : *E. zuluensis*
12,26–31 : *E. albanensis*

p. 150, right column, ref. 26: 'Pith flecks or medullary spots in wood.', not 'Medullary spots in wood.'
p. 150, right column, ref. 29: 'Classifications', not 'Classification'
p. 151, left column, ref. 10: 'SCURFIELD, G.', not 'SCURFIELD, F.L.S.'

NOTES

I would rather consider the macroscopic dark brown or black spots on the transverse surfaces of the studied wood samples simply to be pith flecks and not gum veins. The amorphous material deposited intercellularly in the pith flecks is most probably the remains of dead cells and the excrement of the larvae of the cambium miner—and not gum formed by gummosis of pith fleck parenchyma. However, this suspision needs confirmation.

The crystalliferous tissue encountered in some pith flecks (see Figures 26–30) is undoubtedly derived from the secondary phloem. It becomes incorporated in the pith fleck during the formation of a cambium bridge on the phloem side of the damaged cambium. This is an interesting example of the pathological formation of intraxylary phloem strands. It is, however, unknown to what extent these strands are functional.

Kulman (1964) proposed 'parenchyma fleck' as a more suitable term to replace 'pith fleck' or 'medullary fleck'.

The relatively long discussion devoted to the fact that the crystals (5.3.2.f) are surrounded by a lignified sheeth is perhaps unwarranted. On the strength of a note in Reinders (1951) the formation of thick sheaths enclosing crystals appears to be a common phenomenon in wood. Perhaps this is the reason why it is rarely recorded as such in wood anatomical descriptions. There is nevertheless a need for more information on the taxonomic significance of sclerozed crystalliferous cells in plants.

The starch grains (5.3.2h) were described as hollow and in Figure 51 as collapsed. An alternative state might be that the grains are thimble-shaped.

CHAPTER 6

VAN WYK, A.E., BOTHA, D.J. & COETZEE, J. 1980. The genus *Eugenia* L. (Myrtaceae) in southern Africa: 1. The nature and taxonomic value of the first-formed stem periderm. *Jl S. Afr. Bot.* 46: 67–88.

CORRECTIONS

I regret that the use of English in this paper leaves much to be desired.

p. 70, Table 1: *'E. verdoorniae'*, not *'E. verdoormiae'*
p. 76, caption for Table 3: '. . .Fig. 3 & Fig. 4', not '. . .Fig. 2 & Fig. 3'
p. 79, Table 4, right column: omit '≒ *E. capensis*'
p. 79, para. 6, line 2: 'rank', not 'ranks'
p. 81, Table 5, Character 7: transpose character states
p. 81, para. 1, line 1: 'wish', not 'wishes'
p. 86, caption for Figure 15, line 3: 'phellem', not 'phellum'
p. 86, reference 3: 'DüMMER, R.A.', not 'DüMMER, R.D.'
p. 88, reference 3: 'Dublin : Hodges, Smith & Co.', not 'Kent : L. Reeve & Co. Ltd.'

CHAPTER 8

VAN WYK, A.E. & DEDEKIND, I. The genus *Eugenia* (Myrtaceae) in southern Africa : Morphology and taxonomic value of pollen. *S. Afr. J. Bot.* 51: 371–378.

NOTES

I have now seen a paper by Ong & Rao (1973) on pollen dimorphism in certain flowering plants. Various types of pollen dimorphism are recorded for six homostylous species. References to other reports of pollen dimorphism are also supplied (no Myrtaceae, however).

CHAPTER 9

VAN WYK, A.E. & LOWREY, T.K. 198–. Studies on the reproductive biology of *Eugenia* L. (Myrtaceae) in southern Africa. Submitted for publication in the Proceedings of the 11th AETFAT Plenary Meeting, 10–14 June 1985, St. Louis, U.S.A.

NOTE

I can now confirm the presence of morphological androdioecy in *Decaspermum* (Myrtaceae)—see 4.1, p. 14.

CHAPTER 1 1

VAN WYK, A.E. 1985. Die vlakappel : 'n vergete veldvrug. *Veld & Flora* 71: 18–21.

CORRECTIONS

Unfortunately, I did not see the proofs of this paper. It is the policy of the editor of the journal not to send proofs to the author, but to have the proof-reading done (?) by his editorial staff.

p. 18, column 1, para. 1, line 5: 'daarom', not 'darem'
p. 18, column 1, caption Figs 3 & 4: 'verwyder', not 'vewyder'
p. 18, column 1, para. 2, line 7: 'inheemse', not 'imheemse'
p. 18, column 2, para. 1, line 2: omit 'die'
p. 19, column 1, para. 3, line 1: 'beskrywende', not 'bedrywende'
p. 19, column 1, para. 5, line 5: 'middelland' not 'middellande'
p. 19, column 2, para. 2, line 7: 'nie', not 'bie'
p. 19, column 2, para. 2, line 6: 'uitgebreide', not 'utgebreide'
p. 19, column 3, para. 2, line 14: 'lemoentjie', not 'lemoenetjie'
p. 19, column 3, para. 5, line 5: 'nektar', not 'nektaar'
p. 20, column 1, para. 1, line 12: 'vrugte', not 'bome'
p. 20, column 1, para. 3, line 2: 'vlesig', not 'vleisig'
p. 20, column 3, para. 2, line 5: 'Vroulike', not 'vroulike'
p. 20, column 3, para. 3, line 12: 'Oos-Kaap', not 'Oo-Kaap'
p. 21, column 1, para. 2, line 12: 'the', not 'this'
p. 21, column 1, para. 3, line 4: 'diameter', not 'diamater'
p. 21, column 3, para. 1, line 3: 'vlakappels', not 'vlakapples'

VAN WYK, A.E. 1979. A new species of *Eugenia* L. (Myrtaceae) from southern Natal and Transkei. *Jl S. Afr. Bot.* 45: 273–277.

CORRECTIONS

p. 273, footnote: '1978', not '1979'
p. 277, reference 1: 'DüMMER, R.A.', not 'DüMMER, R.D.'

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VAN WYK, A.E., ROBBERTSE, P.J. & KOK, P.D.F. 1982. The genus *Eugenia* (Myrtaceae) in southern Africa: The structure and taxonomic value of stomata. *Bot. J. Linn. Soc.* 84: 41–56.