Dahlgrenodendron, a remarkable new genus of Lauraceae from Natal and Pondoland

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A reappraisal of the taxonomic relationships of the southern African tree, *Beilschmiedia natalensis* J.H. Ross, proved it to be wrongly placed in the genus *Beilschmiedia* Nees. Its mature fruit is completely covered by the accrescent hypanthium, whereas *Beilschmiedia* (and the tribe Perseeae) is characterized by a completely deciduous perianth. Since it does not fit well with any of the existing lauraceous genera, a new genus, *Dahlgrenodendron* J.J.M. v.d. Merwe & Van Wyk, and new combination, *D. natalense* (J.H. Ross) J.J.M. v.d. Merwe & Van Wyk, are proposed. The pollen is most distinctive and decidedly different from anything known in Lauraceae. Grains are free, radially symmetrical, para-isopolar, \pm spindle-shaped prolate (when dry), atreme, with a wall ornamentation of striae alternating with prominent \pm parallel ridges. *Dahlgrenodendron* is further characterized by opposite leaves, fruit with an endocarp consisting of a palisade of columnar sclereids which develop from the ovary wall, and 2-celled anthers. It is tentatively related to the tribe Cryptocaryeae, subtribe Cryptocaryineae and compared with *Cryptocarya* R. Br. and *Ravensara* Sonn. — the two genera currently constituting this subtribe. *D. natalense* is an exceedingly rare forest species confined mainly to the southern Natal/Pondoland sandstone region. With the total number of individuals probably not exceeding 200, it is considered an ancient relict on the brink of natural extinction.

'n Herwaardering van die taksonomiese verwantskappe van die Suider-Afrikaanse boom, *Beilschmiedia natalensis* J.H. Ross, dui daarop dat dit nie in die genus *Beilschmiedia* Nees tuishoort nie. Die spesie se volwasse vrugte word volkome deur die uitgroeiende hipantium bedek, terwyl *Beilschmiedia* (en die tribus Perseeae) deur 'n volkome afvallende periant gekenmerk word. Aangesien dit nie by enige van die bestaande Lauraceae-genusse inpas nie, word 'n nuwe genus, *Dahlgrenodendron* J.J.M. v.d. Merwe & Van Wyk, en nuwe kombinasie, *D. natalense* (J.H. Ross) J.J.M. v.d. Merwe & Van Wyk, voorgestel. Die stuifmeel van *D. natalense* is besonder kenmerkend en beslis verskillend van enige ander bekend in die Lauraceae. Korrels is vry, radiaal simmetries, para-isopolêr, ± spoelvormigprolaat (wanneer uitgedroog), atreem met 'n wandskulptuur van striasies wat met prominente ± parallel-verlopende riwwe afwissel. *Dahlgrenodendron* word verder gekenmerk deur teenoorstandige blare, vrugte met 'n endokarp bestaande uit 'n palissade van kolomvormige sklereïede wat uit die vrugbeginselwand ontwikkel, en 2-hokkige helmknoppe. Dit word voorlopig met die tribus Cryptocaryeae, subtribus Cryptocaryineae in verband gebring en vergelyk met die twee genusse *Cryptocarya* R. Br. en *Ravensara* Sonn. wat tans laasgenoemde subtribus uitmaak. *D. natalense* is 'n uiters seldsame woudspesie wat grootliks tot die Suid-Natal/Pondoland-sandsteengebied beperk is. Met 'n totale aantal individue van moontlik nie meer as 200 nie, word dit beskou as 'n antieke relik op die rand van natuurlike uitsterwing.

Keywords: Beilschmiedia, Cryptocarya, fruit, Lauraceae, pollen

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Introduction

Beilschmiedia natalensis J.H. Ross is an exceedingly rare forest tree confined mainly to the southern Natal/Pondoland sandstone region. Described by Ross (1973), it was apparently without hesitation assigned to the pantropical genus *Beilschmiedia* Nees. Phytogeographically this isolated record seemed an intriguing case of discontinuity since the nearest species of *Beilschmiedia* occur in west tropical Africa, Uganda, Tanzania and Madagascar. Ross, however, pointed out that *B. natalensis* does not appear to be very closely related to any of the African species.

Recently there has been an increased interest in *B. natalensis* stimulated by an assessment of the floristic affinities of the Natal/Pondoland sandstone endemics and a taxonomic revision of southern African Lauraceae. The discovery in this species of a very peculiar type of pollen unknown elsewhere in Lauraceae, prompted us to take another look at its systematic position.

Palynological and morphological evidence demonstrates that *B. natalensis* does not belong in *Beilschmiedia*. Nor does it exhibit evidence of close relationship to the tribe Perseeae in which this genus is placed by Kostermans (1957). Since it does not fit well into any of the existing lauraceous genera, we have considered it desirable to place it in a genus of its own. This paper summarizes the most pertinent contributions of macromorphology, palynology and fruit and seed structure as the basis for describing the genus *Dahlgrenodendron*. An amplified description of the species is supplied and the required new combination is effected. The proposed new generic name honours the late Prof. R.M.T. Dahlgren, a Swedish systematic botanist of international stature, who took a special interest in the southern African flora.

Descriptions

Dahlgrenodendron *J.J.M. v.d. Merwe & Van Wyk*, gen. nov., probabiliter affine Cryptocaryae et Ravensarae, sed ab his et ab omnibus aliis generibus Lauracearum characteribus sequentibus differt: foliis oppositis, antheris bilocularibus, granulis pollinis para-isopolaribus cum striis conspicuis, ovario uniloculari sine dissepimentis falsis, fructibus omnino ab hypanthio aucto inclusis, endocarpio e pariete ovarii oriundo et e vallo scleroideo uniseriali constanti, et testa partim pachychalazali.

TYPUS.—Dahlgrenodendron natalense (J.H. Ross) J.J.M. v.d. Merwe & Van Wyk, vide infra.

Evergreen trees. *Leaves* opposite; venation brochidodrome. *Inflorescences* with main axis auxotelic or anauxotelic; lateral axes comprising decussately arranged monads or triads.

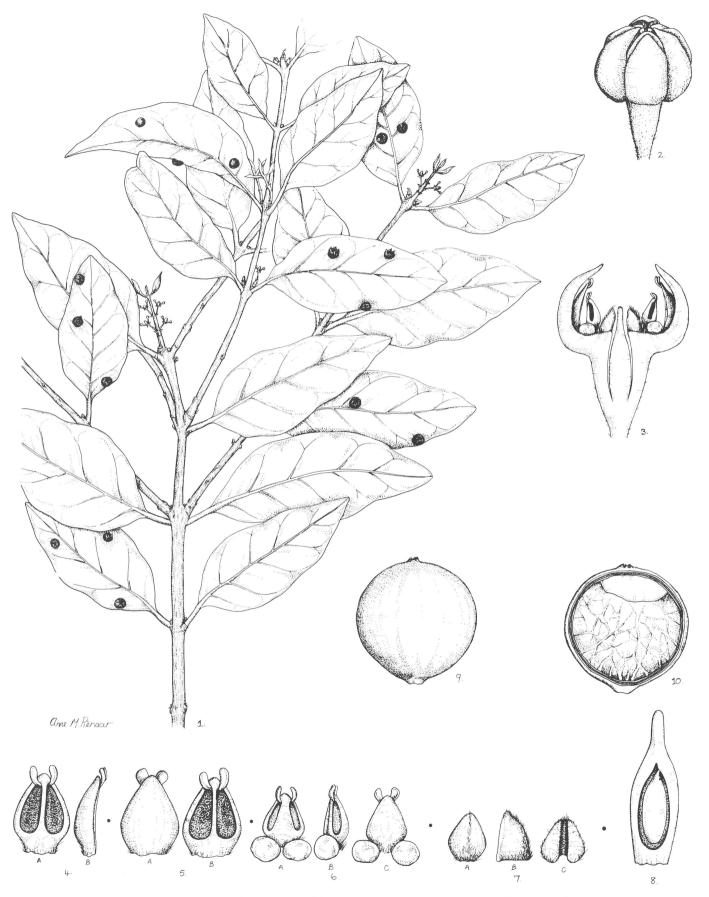


Figure 1 Dahlgrenodendron natalense. 1. Flowering branchlet with some of the leaves showing insect galls, \times 1; 2. flower, partly opened with outer whorl of tepals slightly shorter than the inner, \times 20; 3. flower, longitudinal section (schematic) showing the relative arrangement of the various floral whorls, \times 25; 4–7. androecial whorls (numbered centripetally), different views of fertile stamens and staminodes, all \times 25; 4. stamen of first whorl, ventral (A) and lateral (B) views; 5. stamen of second whorl, dorsal (A) and ventral (B) views; 6. stamen of third whorl — note latrorse-extrose dehiscence and subglobular glands at base, dorsal (A), lateral (B) and ventral (C) views; 7. staminode of fourth whorl — note ventral groove which fits around the style, dorsal (A), lateral (B) and ventral (C) views; 8. ovary, longitudinal section showing the single locule with solitary pendulous ovule, \times 25; 9. fruit — note remains of the tepals at the apex, \times 1,5; 10. fruit, longitudinal section (with embryo removed) showing the relatively thin fruit wall with endocarpal palisade and lower \pm 2/3 of locule lined by the richly vascularized pachychalazal portion of the seed-coat, \times 1,5; (1–8 from Abbott 3324; 9 & 10 from Moll, Cooper & Zaloumis 5668).

Flowers bisexual, trimerous. *Tepals* 3+3. *Fertile stamens* 3+3+3; anthers 2-celled; pollen para-isopolar, striate. *Staminodes* 3. *Ovary* enclosed by the hypanthium, 1-locular with a solitary pendulous ovule; false septa absent. *Fruit* a drupe, completely enclosed by the accrescent hypanthium; fruit wall with endocarp differentiated from the ovary wall (pericarp *s.str.*). *Seed* partly pachychalazal; embryo with 2 massive planoconvex cotyledons; endosperm absent.

Dahlgrenodendron natalense (J.H. Ross) J.J.M. v.d. Merwe & Van Wyk, comb. nov.

Beilschmiedia natalensis J.H. Ross in Bothalia 11: 118 (1973). TYPUS.—Natal: Umdoni Park, 21 December 1971, *Nicholson 1140* (PRE, holotypus!; BOL, E, FHO, K, L, NH!, NU, isotypi).

Evergreen tree up to about 20 m high; bark greyish-brown, scaly, slash dark pinkish-red and slimy; old trees often coppicing from the base of the trunk. Branchlets often laterally flattened (particularly in coppice shoots), green becoming grevish-brown, glabrous with longitudinally elongated lenticels. Leaves petiolate; lamina \pm elliptic to elliptic-ovate, 35 – 100 mm long, 20 - 50 mm wide, base cuneate, apex acute to shortly acuminate, rarely obtuse, coriaceous, dark green, very often with characteristic galls opening mainly on the upper surface; margin entire, often slightly undulate; dried leaves with venation (including the reticulation) prominently raised below, slightly raised but with midrib \pm immersed above; principal lateral veins alternate or opposite, 5-8 pairs; petiole 5-10 mm long, grooved above. Inflorescences axillary on young growth or on reduced brachyblasts, usually composed of \pm decussately arranged cymules; bracts minute; shortly hairy, \pm persistent to caducous. *Flowers* greenish-yellow, c. 2-3 mm diam.; pedicels slender, 2-4 mm long, minutely puberulous. Tepals greenish, ovate-triangular, c. 1,5 mm long, 0,5 mm wide, apex acute, erect-incurved, outer whorl slightly shorter, glabrous or minutely puberulous adaxially, pubescent abaxially towards the base. Fertile stamens \pm ovate-triangular, outer 6 sessile, c. 1 mm long, 0,75 mm wide, apex obtuse, glabrous or abaxially puberulous, adnate to the tepals basally, introrse; 3 inner stamens \pm sessile, c. 0,75 mm long, 0,5 mm wide, apex obtuse, puberulous or slightly puberulous adaxially and towards the base, anthers \pm latrorse to sub-extrorse, each stamen basally flanked by two large sessile, subglobular glands, c. 0,5 mm diam. Staminodes sessile, ovate-triangular, dorsally puberulous, adaxial surface with a longitudinal groove, tightly pressed against the style. Ovary botuliform/ cylindrical, c. 1,75 mm long, 0,5 mm diam., glabrous, gradually merging into a short style c. 0.5 mm long (equalling the staminodes in length); stigma inconspicuous. Fruit \pm globose, c. 20 mm diam., tipped by the persistent remains of the tepals, yellow and occasionally very faintly longitudinally ribbed when ripe; fruit wall leathery, hypanthium part with scattered sclereids, pericarp s.str. with endocarp composed of a palisade of columnar sclereids (see Discussion for a detailed description). Seed globose, overgrown; chalaza extended as a pachychalaza which constitutes the lower 2/3of the seed-coat, the undifferentiated integuments forming the remaining part; embryo without chlorophyll. (Figure 1).

Flowers collected mainly in November/December and fruits in autumn and winter.

Pollen morphology: Pollen shed as monads. Grains radially symmetrical, para-isopolar, prolate to spindle-shaped prolate when dry (SEM), spheroidal when rehydrated (LM), $20-25 \mu m$ equatorial and $25-40 \mu m$ polar diameter (SEM) or *c*. 50 μm diameter (LM), atreme. Intine and exine not

distinguishable in optical section, wall *c*. 5 μ m thick. Sexine surface striate with prominent more or less parallel ridges, apparently subtectate with the ridges consisting of an upper continuous tectal and a lower shortly baculate infratectal part; tectum usually with minute perforations; grooves (striae) intectate. (Figures 3 – 14).

Distribution and habitat

The known geographical distribution of *D. natalense* is shown in Figure 2. First collected at Ngoye Forest in 1961, Ross (1973) also recorded the species from Nqutu Falls west of Krantzkloof Nature Reserve near Durban, Umdoni Park, and near Port Edward in southern Natal. A number of excursions to Ngoye by the second author and others have failed to yield any additional specimens of this species, and it is considered either extremely rare or extinct at this locality. Only one tree is known from Nqutu Falls, but the area is not well collected and may yield additional specimens. At Umdoni Park the species is also known from a single large tree which is obviously slowly dying from old age — this is the plant from which the type material was collected.

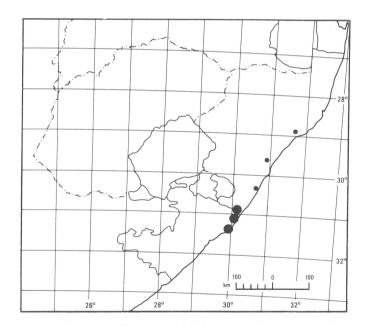


Figure 2 The known distribution of *Dahlgrenodendron natalense*. The three small dots signify relictual occurrences — known only from a single tree at both Umdoni Park and Nqutu Falls and not recollected at Ngoye Forest since the original gathering in 1961. Presently with most individuals (probably less than 200) confined to the southern Natal/Pondoland sandstone region (large dots).

Since 1973 the southern Natal/Pondoland sandstone region has been identified as the major stronghold of *D. natalense*. The largest number of known trees occur in forest relicts scattered from the Msikaba River in Pondoland to just north of the Umtamvuna River in southern Natal (vicinity of Port Edward). The species is nevertheless extremely rare and the total number of mature individuals is estimated at not more than 200.

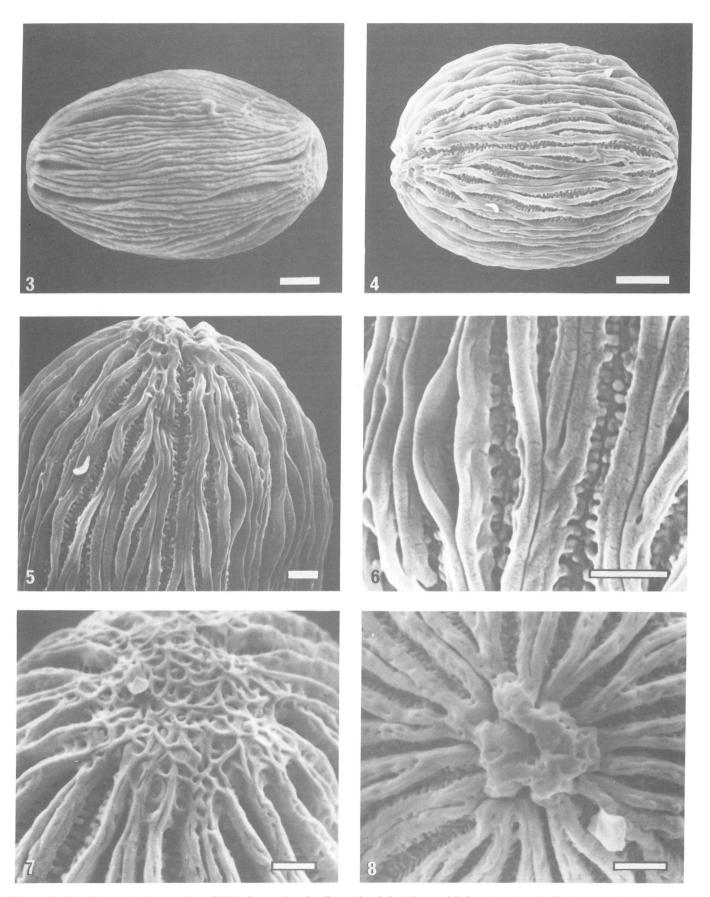
Dahlgrenodendron natalense is associated with sandstone of the Natal Group (probably on granite at Ngoye). It is usually found in forest margins, both next to and away from stream banks. The few specimens recorded from within climax forest were invariably isolated, very old and senescent. No regeneration from seed was recorded in the vicinity of these trees. Reproduction in isolated individuals or small populations

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is probably impaired by a system of synchronous dichogamy which is known to operate in some members of the Lauraceae (see Discussion).

Discussion

Following his thorough and exhaustive revisionary studies in Lauraceae, Kostermans (1957) proposed a new subdivision



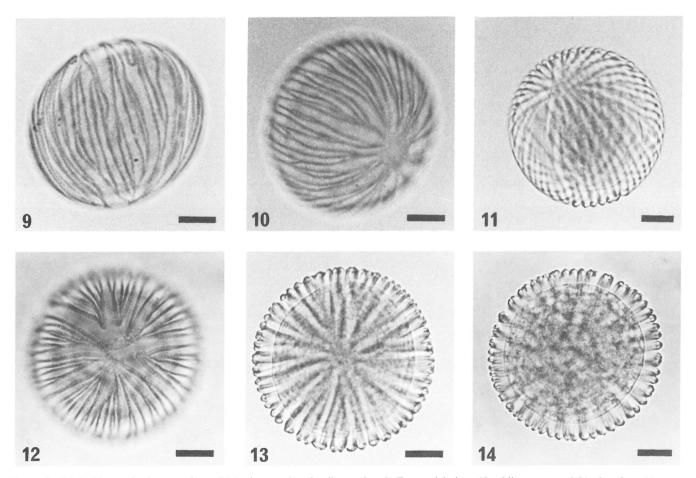
Figures 3 – 8 Dahlgrenodendron natalense. SEM micrographs of pollen grains. **3 & 4.** Equatorial views showing spindle-shaped prolate and prolate shape; **5.** striate ornamentation with ridges ending at pole; **6.** striae and ridges — note short baculae; **7 & 8.** polar views of a grain: grains are para-isopolar with the ornamentation of the two poles slightly different (all from *Van Wyk 5394*; grains unacetolysed, dusted directly from dried anthers onto stubs and sputter-coated with gold). Scale-line = 5 μ m (Figures 3 & 4) or 2 μ m (Figures 5–8).

of the family (for other views on generic relationships within the family see Hutchinson 1964 and Richter 1981). Although it has been pointed out by various authors that distinctions between genera of the Lauraceae are often arbitrary, Kostermans's classification has subsequently gained wide acceptance as well as support from phytochemical evidence (Gottlieb 1972). Judged on macromorphology alone, the affinities of *Dahlgrenodendron* appear to centre around the genera of the tribes Perseeae and Cryptocaryeae. Comparisons which follow will therefore be mainly with genera of these two groups.

For the segregation of tribes, Kostermans considered the development of the hypanthium (floral tube) in the fruit of primary importance. A perianth that is completely deciduous in the fruit characterizes the tribe Perseeae. Hence the ripe fruit is not surrounded by extracarpellary tissue, not even in the form of a basal cupula. *Beilschmiedia*, a well-defined genus as to its fruit characters and 2-celled anthers, is the largest genus of this tribe and constitutes the only member of the subtribe *Beilschmiediinae*. Ripe fruit of *Dahlgreno-dendron natalense* is completely enclosed in and adnate to the accrescent hypanthium. It should therefore be excluded from the Perseeae. Despite the availability of fruiting material, Ross (1973) apparently overlooked this character when he described this species in *Beilschmiedia*.

In Kostermans's (1957) system, the tribe Cryptocaryeae accommodates all those members of the Lauraceae with the ovary superior but with the fruit completely included in the accrescent hypanthium. Accordingly, *Dahlgrenodendron* keys out as belonging to this tribe and, on account of its 2-celled anthers, more specifically the subtribe Cryptocaryineae. In this subtribe Kostermans recognized two genera, namely *Ravensara* Sonn. and *Cryptocarya* R. Br. *Ravensara* is a small but distinctive genus endemic to Madagascar. It can easily be separated from related genera by its fruit which has the basal part of the locule divided into 6(12) compartments by 6(12) false dissepiments (remains of the nucellus?). This would leave *Cryptocarya* as the only currently recognized genus to which *Beilschmiedia natalensis* could be relegated. Our reasons for not having taken this step will next be argued on the basis of evidence derived mainly from pollen morphology and fruit structure.

Among primitive angiosperms, pollen morphology has proven to be especially useful in providing indications of affinity in the Monimiaceae (e.g. Schodde 1970; Thorne 1974; Walker 1976a; Lorence *et al.* 1984). It is therefore surprising that palynological characters have hitherto attracted virtually no attention for defining groups in the closely related Lauraceae. Admittedly, the few lauraceous taxa so far studied have rather invariant pollen. These have been described as more or less spheroidal, apolar, inaperturate and spinulose (Erdtman 1952; Veloso & Barth 1962; Wang 1969; Mitroiu 1970; Walker 1976a, b; Datta & Chanda 1980) (Figures 15 & 16). In addition, the exine is highly reduced and consists only of a thin coherent layer ornamented with spines and globules. The intine is composed of an unstratified inner and a thick



Figures 9–14 Dahlgrenodendron natalense. LM micrographs of pollen grains. 9. Equatorial view; 10. oblique equatorial/polar view; 11. same view as in 10 but with greater depth of field showing spheroidal shape and surface with \pm parallel ridges converging at the poles; 12. polar view; 13. polar view and optical section — striae converging at the pole faintly visible; 14. polar view with optical cross-section at equatorial level — note undifferentiated wall and prominent ridges (all from *Van Wyk 5394*; grains unacetolysed and mounted in glycerine jelly). Scale-line = 10 µm.

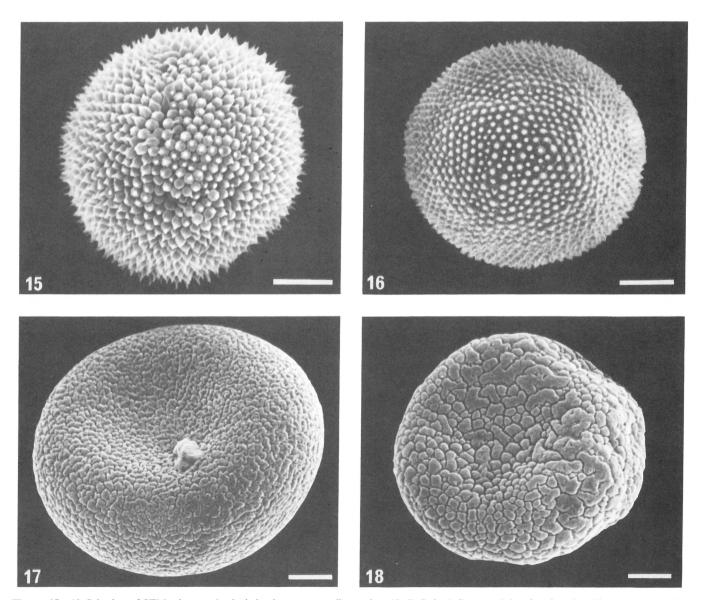
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outer layer with tubular ultrastructure (Hesse & Kubitzki 1983; for an older interpretation see Kubitzki 1981).

However, Cryptocarya pollen differs from this generalized pattern in being peroblate/oblate (when rehydrated) and circular in outline, with a more or less smooth or slightly verrucate exine surface. In SEM the grains are strongly flattened, and often more or less biconcave, circular discs (discshaped oblate) — almost resembling red blood cells (unpublished observations on some African and Madagascan species; Figures 17 & 18). Unfortunately we were unable to study pollen grains of the opposite-leaved Madagascan species of Cryptocarya (see below). In its pollen Dahlgrenodendron differs markedly from all other investigated members of the Lauraceae. Striate pollen is very rare among primitive angiosperms (Walker 1976a, b) and we could not find reports of grains resembling those of Dahlgrenodendron among any of these families. The striking difference in shape between dehydrated and rehydrated grains suggests that the striate ornamentation of the exine may be a harmomegathic mechanism ensuring the extended survival of the grains during phases

of desiccation and rehydration (e.g. Muller 1979; Blackmore & Barnes 1986; Thanikaimoni 1986). The extraordinary more or less parallel tectate ridges in the grains of this genus may well be the homologues of the semihelical bands reported for Hortonia Wight, or the striato-rugulate exine configurations in species of Phanerogonocarpus Cavaco and Tambourissa Sonn. — all members of the Monimiaceae (Money et al. 1950; Lorence et al. 1984). At this stage it is also not clear whether it is correct to consider the short infratectal rods supporting the tectate ridges in Dahlgrenodendron as columellae (baculae). A detailed study of pollen-wall architecture in this genus is currently under way and will be reported elsewhere. From the diversity encountered among pollen grains of the Lauraceae in the present study, it is nevertheless clear that pollen morphology should be important in any future subdivision of the family.

As a member of the Cryptocaryeae, the fruit of *Crypto-carya* is completely covered by the accrescent hypanthium. In external morphology the fruit of *Dahlgrenodendron* (Figure 19) resembles that of *Cryptocarya*, although the tepals



Figures 15-18 Selection of SEM micrographs depicting lauraceous pollen grains. 15. *Beilschmiedia mannii* showing densely echinate ornamentation typical of African members of the genus (*Leonard 249* in PRE); 16. *Ocotea bullata* showing spinulose ornamentation commonly encountered in *Ocotea* and many other genera of the family (*Van der Merwe 597* in PRU); 17. *Cryptocarya wyliei* with non-spinuliferous and disc-shaped oblate grain type recorded in African and at least some Madagascan species of this genus (*Van der Merwe 600* in PRU); 18. *Cryptocarya woodii* showing disc-shaped oblate shape and rugulose exine surface (*Van der Merwe 601* in PRU); grains unacetolysed; obtained from dried anthers and sputter-coated with gold prior to viewing). Scale-line = 4 μ m.

persisting at the tip of the fruit are deciduous in some species of the latter genus. Fruit which ripens yellow, as in *Dahlgrenodendron*, is rare in the Lauraceae. Black or red is the prevailing colour in most members of the family (Kostermans 1957) and at least all African species of *Cryptocarya*. Structurally, however, there are major differences between the fruit of these two genera. In the subsequent discussion the term pericarp is used for the matured ovary wall (pericarp *s.str*. of some authors) only. Extracarpellary tissue surrounding the immersed pericarp is referred to as the hypanthium. The term fruit wall denotes the combination of pericarp and hypanthium. Ovule-derived tissue enveloping the seed is referred to as the seed-coat. Unless indicated otherwise, seed terms follow Corner (1976).

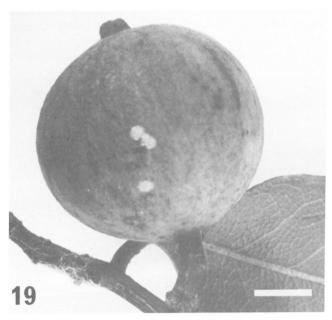
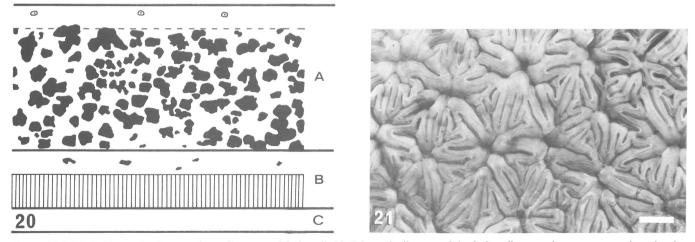


Figure 19 Dahlgrenodendron natalense. Almost-ripe fruit completely enclosed by the accrescent hypanthium (floral tube) — note tepals persisting at the apex (*Abbott 3944*). Scale-line = 5 mm.

The mature fruit wall of Cryptocarya consists of a relatively thin but succulent outer part and a bony inner part of variable thickness. In most African species this bony layer is already well developed in the very young fruit, and its presence often makes it impossible or very difficult to cut through the fruit wall with a knife. The bony layer recalls an endocarp but develops entirely from the inner part of the hypanthium. It consists of a broad zone of densely packed brachysclereids. The pericarp remains parenchymatous, very thin and undifferentiated. In the material examined, the chalaza extended as a pachychalaza to form about two-thirds of the length of the seed. The seed-coat remains thin and undifferentiated (mechanical layer absent), although the pachychalazal portion is pervaded by a network of tracheoid (sensu Schmid 1986) strands and the integumentary portion (both testa and tegmen) is slightly multiplicative.

In Dahlgrenodendron the texture of the mature fruit wall (Figure 20) can perhaps best be described as leathery. The subepidermal layers are slightly fleshy but not succulent as in Cryptocarya. With the exception of this thin parenchymatous peripheral part, the remainder of the hypanthium consists mainly of parenchyma cells interspaced with numerous, more or less isolated, brachysclereids. The latter cells are not densely packed and, in contrast to Cryptocarya, this sclereid-containing zone does not resemble an endocarp. It can easily be cut with a knife. *Dahlgrenodendron* is also quite different from Cryptocarya in having a differentiated pericarp. The endocarp develops from the inner epidermis of the pericarp and consists of a single-layered palisade of columnar, thick-walled and lignified cells with stellate-undulate facets (Figure 21). Such endocarpal sclereids with wavy walls are typical for the Lauraceae (Corner 1976; Roth 1977). The seed has a well-developed pachychalaza constituting about twothirds of the seed-coat, and thereby resembling Cryptocarya. The principal structural difference between the mature fruit wall of the two genera can be summarized as follows: in Cryptocarya the main mechanical tissue develops from the inner parts of the hypanthium and consists of a broad zone of densely packed brachysclereids, whereas in Dahlgrenodendron there is a proper endocarp consisting of a palisade of columnar sclereids which develop from the inner epidermis



Figures 20 & 21 *Dahlgrenodendron natalense.* Structure of fruit wall. **20.** Schematic diagram of the fruit wall as seen in transverse section, showing the different layers and the relative proportion occupied by each; A = hypanthium with outer parenchyma portion shown with three secretory cells, broad inner parenchyma portion with numerous solitary and clustered brachysclereids (black); B = pericarp (ovary wall) with inner epidermis differentiated into a single-layered palisade of columnar sclereids, parenchyma zone with occasional brachysclereids (black); C = seed-coat, parenchymatous with pachychalazal portion pervaded by tracheoid strands; **21.** endocarp (inner zone of layer B in Figure 20) in transverse section showing sclereids with minute lumina and very wavy outlines (both figures from *Moll, Cooper & Zaloumis 5668*). Layer B = 0,18 mm (Figure 20) or scale-line = 100 μ m (Figure 21).

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of the pericarp. Fruit structure is still comparatively little known in the Lauraceae. As with pollen morphology, it may serve as a useful check on generic alliances in the family.

In the Lauraceae characters of vegetative morphology are not very useful for the delimitation of genera. Dahlgrenodendron differs from all African members of the family in its consistently opposite leaves. Despite this arrangement being uncommon in the family, it is not always a generic character as alternate, subopposite and whorled leaves may be found in species of the same genus (Kostermans 1957). Opposite leaves have for example been recorded in most American species of Beilschmiedia and in about four Madagascan species of Cryptocarya - two genera with a predominantly alternate arrangement. At present the relationships between the latter species of Cryptocarya and Dahlgrenodendron are not clear. Unfortunately we were unable to examine fertile material of these species. Should future studies show them to resemble Dahlgrenodendron in fruit and pollen morphology, a transfer to this genus would not create nomenclatural problems since no older generic names will be involved. In wood anatomy, some of the Madagascan species of Cryptocarya do not appear to belong in Cryptocarya (Richter 1981). The wood anatomy of Dahlgrenodendron (Swart 1986) suggests that a close relationship with these Madagascan species is very unlikely (also Richter pers. comm.).

A very characteristic type of insect gall is usually present on the leaves of *D. natalense* (Figure 1). The identity of the insect is still unknown, but the galls appear to be of the same type as those found on *Ocotea bullata* (Burch.) E. Mey. These (not to be confused with the domatia in the axils of the secondary veins) are caused by one of the Psyllidae (Story 1951).

The same basic floral structure is shared by various genera in the Lauraceae. Hence floral characters are of little taxonomic value for determining relationships above the species level. Dahlgrenodendron displays a basic floral structure widespread within the Lauraceae, especially in Beilschmiedia and the tribe Cryptocaryeae. These apparently shared ancestral features supply little or no useful information about its near relationships. Placing too much emphasis on these may also obscure the preponderance of dissimilarities in other features. A floral construction similar to that of *Dahlgrenodendron* is linked with a particular system of synchronous dichogamy hitherto recorded in a few lauraceous genera (Kubitzki & Kurz 1984) including Cryptocarya (unpublished observations), and which is probably of widespread occurrence in the family. We suspect that this type of dichogamy may also prevail in Dahlgrenodendron. Populations of D. natalense are small and usually widely discontinuous in their distribution. The scarcity of the species may, at least in part, reflect a difficulty to achieve optimal fruit-set. This possibility should be taken into account in any future efforts aimed at the conservation of the species.

Pending further studies, particularly on the opposite-leaved Madagascan species of *Cryptocarya*, we provisionally place *Dahlgrenodendron* in the tribe Cryptocaryeae, subtribe Cryptocaryineae. However, once evidence from comparative studies on these and other little-known members of the family becomes available, its possible placement in a new subtribe or tribe of its own should be considered.

Any judgement concerning the floristic affinities of taxa endemic to a region depends greatly upon taxonomic concepts. *D. natalense* is one of an exceptionally high number of woody species endemic to, or concentrated in the relatively small southern Natal/Pondoland sandstone region. It has been

hypothesized that some of these taxa are relict elements of the Cretaceous/Tertiary forest flora which were present in this part of Gondwana (van Wyk 1985). A comprehensive exposition of this hypothesis, including a discussion of the phytogeographical significance of the available evidence is awaiting the description of several newly recorded taxa as well as the critical re-evaluation of the taxonomic status of previously described ones. With the recent transfer of Rhynchocalyx lawsonioides Oliv. from Lythraceae to its own newly established family (Johnson & Briggs 1984), the southern Natal/Pondoland sandstone region now boasts one monotypic endemic family (Rhynchocalycaceae) and no less than six monotypic genera endemic to or largely confined to this centre of endemism (Dahlgrenodendron, Eriosemopsis Robyns, Jubaeopsis Becc., Pseudosalacia Codd, Pseudoscolopia Gilg and Rhynchocalyx Oliv.). All of these appear to be taxonomically isolated taxa on the brink of natural extinction. They show all the features of palaeoendemics and are seen as relicts derived from the Cretaceous/Tertiary forest flora prevailing in this part of Gondwana. In this connection Dahlgrenodendron is regarded as a surviving representative of the ancestral stock from which Cryptocarya, Ravensara and perhaps some members of the Monimiaceae alliance have evolved.

Specimens examined

—2831 (Nkandla): Ngoye Forest (– DC), *Wells & Edwards 120* (NH, PRE).

—2930 (Pietermaritzburg): Nqutu Falls, just west of Krantzkloof Nature Reserve (–DB), *Cooper 49* (NH, PRE), *Moll, Cooper & Zaloumis 5668* (NH, PRE).

-3030 (Port Shepstone): Umdoni Park (-BC), Cooper 40 (PRE), Nicholson 694 (PRE) & 1140 (NH, PRE), Strey 10578 (NH, PRE), Van Wyk 1375 (PUC); Umtamvuna Nature Reserve [UNR], Beacon Hill (-CC), Nicholson 1228 (NH, PRE), Van Wyk 5033 (PRU).

—3129 (Port St. Johns): Mkambati Game Reserve, Mkambati River (–BD), *Schrire, Van Wyk & Abbott 1807* (NH, PRU).

-3130 (Port Edward): UNR, Amphitheatre (-AA), *Abbott 24 & 3944* (PRU), *Van Wyk 5381* (PRU) & *5394* (PRE, PRU); UNR, tributary of the Bululu River (-AA), *Van Wyk 4204* (PRU); UNR, Clearwater/ Blencathra (-AA), *Abbott 631* (PRU); UNR, Citadel (-AA), *Abbott 2840* (PRU); UNR, Bululo River (-AA), *Abbott 3324* (PRU); Forster's Kloof, Craigadour Farm (-AA), *Nicholson 1227* (NH); Sikuba River, tributary of the Mzamba River (-AA), *Abbott 3184* (PRU), *Van Wyk 7409* (PRU).

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References

- BLACKMORE, S. & BARNES, S.H. 1986. Harmomegathic mechanisms in pollen grains. In: Pollen and spores, eds Blackmore, S. & Ferguson, I.K. Linnean Society symposium series no. 12, pp. 137–149, Academic Press, Cambridge.
- CORNER, E.J.H. 1976. The seeds of dicotyledons. Vols 1 & 2, Cambridge University Press, Cambridge.
- DATTA, K. & CHANDA, S. 1980. Pollen morphology of a few members of the order Laurales (*sensu* Takhtajan 1969) with reference to taxonomy and phylogeny. *Trans. Bose Res. Inst.* 43: 73-79.

- ERDTMAN, G. 1952. Pollen morphology and plant taxonomy, 1st edn, Almquist & Wiksell, Stockholm.
- GOTTLIEB, O.R. 1972. Chemosystematics of the Lauraceae. *Phytochem.* 11: 1537-1570.
- HESSE, M. & KUBITZKI, K. 1983. The sporoderm ultrastructure in *Persea, Nectandra, Hernandia, Gomortega* and some other Lauralean genera. *Pl. Syst. Evol.* 141: 299-311.
- HUTCHINSON, J. 1964. The genera of flowering plants. Clarendon Press, Oxford.
- JOHNSON, L.A.S. & BRIGGS, B.G. 1984. Myrtales and Myrtaceae — a phylogenetic analysis. *Ann. Mo. Bot. Gdn* 71: 700-756.
- KOSTERMANS, A.J.G.H. 1957. Lauraceae. *Reinwardtia* 4: 193-256.
- KUBITZKI, K. 1981. The tubular exine of Lauraceae and Hernandiaceae, a novel type of exine structure in seed plants. *Pl. Syst. Evol.* 138: 139-146.
- KUBITZKI, K. & KURZ, H. 1984. Synchronized dichogamy and dioecy in neotropical Lauraceae. *Pl. Syst. Evol.* 147: 253 – 266.
- LORENCE, D.H., ZENGER, V.E. & VINAY, P. 1984. Pollen morphological studies on the Monimiaceae in the Malagasy region. *Grana* 23: 11–22.
- MITROIU, N. 1970. Études morphopolliniques et des aspects embryologiques sur les 'Polycarpicae' et Helobiae avec des considérations phylogénétiques. Acta Bot. Horti Bucarest. 1969: 3-241.
- MONEY, L.L., BAILEY, I.W. & SWAMY, B.G.L. 1950. The morphology and relationships of the Monimiaceae. *J. Arnold Arbor.* 31: 372–404.
- MULLER, J. 1979. Form and function in angiosperm pollen. Ann. Mo. Bot. Gdn 66: 593-632.
- RICHTER, H.A. 1981. Anatomie des sekundären Xylems und der Rinde der Lauraceae. Sonderbände des Naturw. Ver. Hamburg:5. Verlag Paul Parey, Hamburg.
- ROSS, J.H. 1973. Lauraceae: A new generic record for South Africa and a new species. *Bothalia* 11: 118.
- ROTH, I. 1977. Fruits of angiosperms. Borntraeger, Berlin.

- SCHMID, R. 1986. On Cornerian and other terminology of angiospermous and gymnospermous seed coats: historical perspective and terminological recommendations. *Taxon* 35: 476-491.
- SCHODDE, R. 1970. Two new suprageneric taxa in the Monimiaceae (Laurales). *Taxon* 19: 324-328.
- STORY, R. 1951. New distribution for Ocotea bullata E. Mey, and Lachnopylis floribunda (Bth.) C.A. Sm. with an account of an insect pest of stinkwood. S. Afr. J. Sci. 47: 190–198.
- SWART, J.P.J. 1986. 'n Sistematies-houtanatomiese ondersoek van die Lauraceae in Suidelike Afrika. M.Sc. thesis, Univ. of Stellenbosch.
- THANIKAIMONI, G. 1986. Pollen apertures: form and function. In: Pollen and spores, eds Blackmore, S. & Ferguson, I.K., Linnean Society symposium series 12, pp. 119–136, Academic Press, London.
- THORNE, R.F. 1974. A phylogenetic classification of the Annoniflorae. *Aliso* 8: 147-209.
- VAN WYK, A.E. 1985. The sandstone region of southern Natal and Pondoland: a remarkable centre of endemism. Summary, In: Abstracts of the A.E.T.F.A.T. 11th Plenary Meeting, 10-14 June 1985, p. 33, Missouri Botanical Garden, St. Louis, Missouri, U.S.A.
- VELOSO, H.P. & BARTH, O.M. 1962. Catálogo sistemático dos póllens das plantas arbóreas do Brasil meridional: I. Magnoliaceae, Annonaceae, Lauraceae e Myristicaceae. *Mem. Inst. Oswaldo Cruz.* 60: 59–90.
- WALKER, J.W. 1976a. Evolutionary significance of the exine in the pollen of primitive angiosperms. In: The evolutionary significance of the exine, eds Ferguson, I.K. & Muller, J., Linnean Society symposium series 1, pp. 251–308, Academic Press, London.
- WALKER, J.W. 1976b. Comparative pollen morphology and phylogeny of the ranalean complex. In: Origin and early evolution of angiosperms, ed. Beck, C.B. pp. 241–299, Columbia University Press, New York.
- WANG, J-L. 1969. Morphological study on the pollen grains of Laurales of Taiwan. Bull. Taiwan Forest Res. Inst. 175: 1-36.