

A new species of *Combretum* from Venda and taxonomic notes on the section *Angustimarginata* (Combretaceae)

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Combretum vendae Van Wyk, a shrub or small tree endemic to the central mountainous region of Venda, is described. It belongs to section *Angustimarginata* Engl. & Diels and can be distinguished from related species mainly by its leaf blades with conspicuously raised venation and dense whitish indumentum on the lower surface.

Section *Angustimarginata* is a natural taxon of closely related species restricted to southern Africa. The following additional species are upheld: *C. caffrum* (Eckl. & Zeyh.) Kuntze, *C. erythrophyllum* (Burch.) Sond., *C. kraussii* Hochst., *C. nelsonii* Duemmer and *C. woodii* Duemmer.

Notes are given on diagnostic characters, species delimitation and possible interspecific relationships within the section. A key to the species of section *Angustimarginata* as well as a selection of representative specimens for each species are provided.

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Combretum vendae Van Wyk, 'n struik of kleinerige boom endemies in die sentrale bergagtige gebied van Venda, word beskryf. Dit behoort tot die seksie *Angustimarginata* Engl. & Diels en kan hoofsaaklik op grond van die blaarlaminas met opvallende verhewe bearing en digte witterige haarkleed op die onderoppervlak, van verwante spesies onderskei word.

Seksie *Angustimarginata* is 'n natuurlike takson bestaande uit naverwante spesies wat almal tot suidelike Afrika beperk is. Die volgende addisionele spesies word erken: *C. caffrum* (Eckl. & Zeyh.) Kuntze, *C. erythrophyllum* (Burch.) Sond., *C. kraussii* Hochst., *C. nelsonii* Duemmer en *C. woodii* Duemmer.

Diagnostiese kenmerke, spesie-omgrensing en moontlike interspesifieke verwantskappe in die seksie word bespreek. 'n Sleutel tot die spesies van seksie *Angustimarginata*, asook voorbeelde van verteenwoordigende eksemplare vir elke spesie, word voorsien.

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1. Introduction

A recent floristic survey of the Republic of Venda has yielded an interesting new species of *Combretum* Loeffl. apparently not previously collected. Vegetatively it is somewhat reminiscent of *C. collinum* Fresen. subsp. *gazense* (Swynnerton & Bak.f.) Okafor, *C. moggii* Exell and *C. molle* R. Br., but this resemblance was soon found to be superficial. Examination of the glandular scales clearly revealed a relationship with section *Angustimarginata* Engl. & Diels (*sensu* Stace 1969 *et* Exell 1970, 1978).

Section *Angustimarginata* is restricted to southern Africa and includes the two widespread species *C. erythrophyllum* (Burch.) Sond. (for synonymy see Exell 1978) and *C. kraussii* Hochst. In addition to these (and apart from the new species), I accept as distinct the following species which show a more restricted geographical distribution: *C. caffrum* (Eckl. & Zeyh.) Kuntze (= *Dodonaea caffra* Eckl. & Zeyh. and *C. salicifolium* E. Mey.), *C. nelsonii* Duemmer and *C. woodii* Duemmer (*p.p. quoad* syntype Galpin 1176). Species delimitation within the section is rather difficult because the species are closely related and somewhat variable.

I have studied all the herbarium specimens of *Combretum*, particularly those of section *Angustimarginata*, in PRE and PRU. Extensive fieldwork has enabled me to investigate populations of all the relevant species as an aid in evaluating their taxonomic status. This paper provides a description of the new species from Venda as well as notes on the delimitation of species and possible interspecific relationships within the section. This study is not intended as a taxonomic revision but rather as a framework from which a formal revision of the section can commence.

2. Description

Combretum vendae Van Wyk, **sp. nov.**; differt a speciebus ceteris subgen. *Combreti* sect. *Angustimarginatorum* paginis inferioribus foliorum indumentum dense lanatum et venas conspicue elevatas praebentibus.

TYPE. — Venda, 2230 (Messina): Vuvha, north-east of Thengwe, near the village Muledzhi (–DA), Van Wyk 3913 (PRU, holo.; K; P; PRE).

Shrub usually 1.5–3 m high, rarely a small slender tree up to 5 m high, deciduous or semi-deciduous; bark ± smooth, grey. Branches densely tomentose with whitish or greyish indumentum persisting until the bark is shed. Leaves opposite

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Figure 1 *Combretum vendae*. 1. Fruiting twig ($\times 1$) with part of a lamina enlarged to show the prominent venation on the lower surface — indumentum not shown (Van Wyk 3913); 2. Inflorescences, $\times 1$; 3. Flower, $\times 8$; 4. Longitudinal section of flower with petals and stamens removed, $\times 8$ (all from Van Wyk & Theron 4934).

or very rarely ternate; lamina elliptic, broadly elliptic, obovate or oblanceolate, (30)40–80(100) mm long, (15)25–45(55) mm wide, base cuneate, subrotund, rarely rotund or subcordate, apex obtuse, rounded, acute and apiculate or mucronate (usually twisted), very rarely retuse, initially covered by dense whitish or greyish indumentum, very rarely becoming nearly glabrous or glabrous below, becoming sparingly pubescent or glabrous above (except for scales), usually densely and conspicuously lepidote above when mature; first leaves in spring often temporary partly or completely bleached above, dark green or greyish green and usually \pm discolorous (owing to the indumentum below) when mature; venation (including the reticulation) usually slightly immersed but the midrib \pm raised above, very prominently raised below; principal lateral veins alternate or opposite, 5–8 pairs; petiole 2–3(5) mm long, tomentose. *Inflorescences* of short axillary subcapitate spikes (10)15–20(25) mm long, very rarely forming short panicles by the suppression of leaves on short shoots; peduncle and rachis whitish or greyish tomentose; bracts up to 2 mm long, \pm linear, caducous. *Flowers* 4-merous, light yellow or cream, \pm congested. *Lower receptacle* ca. 1,5 mm long, 1 mm wide, tomentose. *Upper receptacle* ca. 3 mm long, 4 mm wide, visibly divided into a lower \pm tubular part containing the disk and an expanded \pm cupuliform upper part, pubescent, with numerous scales visible towards the apices of the sepals where the indumentum is not so dense. *Sepals* usually tinged reddish purple, ca. 1 mm long, \pm deltate. *Petals* ca. 2,5 mm long, 1,5 mm wide, narrowly obovate, oblanceolate or elliptic, unguiculate, glabrous or very rarely with a few scattered hairs on the margin at the apex. *Stamens* 8, \pm 1-seriate, inserted shortly above the margin of the disk; filaments ca. 6 mm long; anthers ca. 0,8–0,9 mm long. *Disk* free for ca. 0,5 mm; glabrous with a pilose margin. *Style* ca. 5 mm long. *Fruit* (3)4-winged, flushed with pink or red often completely turning dark wine-red, ca. 16–22 mm long, 12–15 mm wide, elliptic, broadly elliptic or subcircular in outline, lepidote, apical peg ca. 0,5 mm long or absent, wings up to 6 mm wide, stipe 4–7 mm long. *Cotyledons* 2, epigeal. *Scales* conspicuous on mature leaves (often whitish) and very numerous (occasionally almost contiguous) above, often concealed by glutinous secretions in young leaves, absent or very rarely present (then sparse) below (usually obscured by the indumentum), ca. 50–60 μ m diam., \pm circular although often with the outline slightly and irregularly undulate, delimited by (10–) 16 primary radial walls alone, outer tangential cell walls usually slightly convexly scalloped. *Interxylary phloem* present as scattered strands in older stems (often not found in herbarium material) (Figure 1).

Flowering takes place in spring, mainly between mid-September and mid-October and ripe fruits are produced in autumn and winter.

3. Distribution and Habitat

The first collection of *C. vendae* was made as recently as April 1980 at Vuvha, north-east of Thengwe on the south facing slopes of the main eastern outlier of the Soutpansberg mountain range. Several subsequent excursions to Venda have established a distributional range for the species stretching from Vuvha south-westward to Fefe (Figure 2).

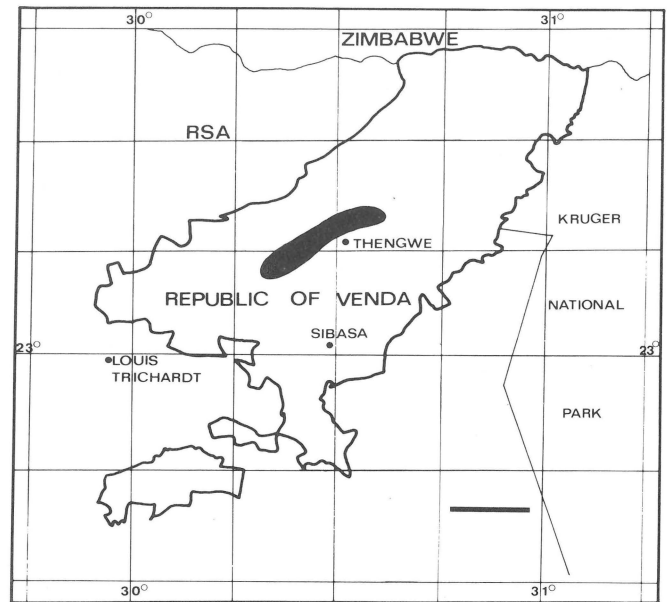


Figure 2 The known distribution (black area) of *Combretum vendae*. Bar = 20 km.

Botanically the mountains east of Vuvha are virtually unexplored and may yield additional records for the species.

C. vendae occurs, often in abundance, on the plateaux and higher eastern and southern slopes of the mountain range. The climate grades from relatively dry and hot at Vuvha to relatively moist (but still too dry for the development of forest) and mild conditions at Fefe. Rainfall occurs mainly during summer and mild winters without frost are experienced. No rainfall figures are available for the region. Mist occurs frequently, especially during summer.

The predominant rock type of the area is sandstone. *C. vendae* favours rocky sandy soil as well as regions of deep red sandy soil (probably eolian) which are scattered throughout the area.

The vegetation types of which *C. vendae* forms a part can be described as a mosaic of short // low thicket and short // low bushland (Edwards 1983). Floristically the woody component of the vegetation is often exceptionally heterogeneous, particularly in the mountainous terrain north-east of Thengwe. Species of *Combretum* often associated with *C. vendae* include *C. apiculatum* Sond., *C. hereroense* Schinz, *C. moggii*, *C. molle*, *C. mossambicense* (Klotzsch) Engl., *C. zeyheri* Sond. and especially *C. collinum* subsp. *gazense*. From a distance *C. vendae* is almost indistinguishable from the last-named species on account of its shrubby habit and dark greyish green leaves. However, in autumn *C. vendae* is quite conspicuous owing to the wine-red colour of its fruits.

No other species of section *Angustimarginata* is associated with *C. vendae*. *C. kraussii* is common in patches of forest south-east of Fefe, especially between Rambuda and Tate Vondo, and in the area surrounding Lake Fundudzi. The distribution of these two species is clearly discontinuous and no cline has been observed in the field.

4. Specimens Examined

VENDA. — 2230 (Messina): Fefe (–CB), Van Wyk 5667 (BM; PRE; PRU; VENDA); Ha-Mabila (–CB), Van Wyk 5676, 5677 (both K; P; PRE; PRU; VENDA), 5678 (PRE; PRU; SRGH), 5946 (PRE; PRU), 5947 (COI; PRU), 5948 (PRE; PRU), 5949 (BM; PRU);

Mountain plateau at Tsharokho north of Thengwe (-DA), Carr 200 (PRE; PRU), 201 (K; PRU; VENDA), Van Wyk 5640 (PRE; PRU; VENDA), 5641 (C; MO; PRE; PRU), 5642 (COI; PRU; SRGH), 5643 (P; PRE; PRU), 5644 (K; NH; PRU); Savhani (-DA), Van Wyk 5682 (K; PRE; PRU); Vuvha, north-east of Thengwe near the village Muledzhi (-DA), Van Wyk 3913 (PRU, holo.; K; P; PRE), 5573 (COI; K; PRE; PRU; SRGH), 5574 (PRE; PRU), 5575 (BM; C; P; PRE; PRU; VENDA), 5576 (PRE; PRU), 5577 (MO; PRE; PRU), 5579 (PRE; PRU), 5580 (BM; K; PRU), 5581 (NH; PRU; SRGH), 5582 (C; PRE; PRU), 5584 (PRE; PRU), 5585 (NH; PRE; PRU), 5592 (MO; PRU), Van Wyk & Theron 4923 (BM; COI; K; P; PRE; PRU), 4924 (K; PRE; PRU), 4927 (PRE; PRU), 4928 (K; PRE; PRU), 4934 (K; PRU; VENDA); Thengwe, ± 0.5 km north of turnoff to Tshikundamalema on the road to Mafukani (-DA), Van Wyk 5634 (C; COI; PRU), 5635 (NH; PRE; PRU; SRGH); Mufulwi, near Thengwe/Fundudzi road junction (-DA), Van Wyk 5952 (K; PRU).

5. Discussion

5.1 Diagnostic characters of *C. vendae* and miscellaneous notes on section *Angustimarginata*

C. vendae is without doubt the most distinctive species within section *Angustimarginata*. It can easily be distinguished by its leaf blades with conspicuously raised venation (including the venule reticulum) and dense whitish indumentum of combretaceous hairs on the lower surface. The former character appears to be constant but the latter has some variability in a small population found near the village Muledzhi, between Thengwe and Tshikundamalema, where leaves ranging from almost glabrous (e.g. Van Wyk 5573) to densely tomentose (e.g. Van Wyk 5592) have been found. The almost glabrous condition is, however, extremely rare and may be considered anomalous.

Section *Angustimarginata* may be regarded as a homogeneous and very natural taxon. The following sectional characters can be added to those supplied by Exell (1970, 1978): bark more or less smooth or flaking in small, rather papery pieces in very old stems; the first leaves in spring with the upper surface partly or completely cream-coloured (apparently without chlorophyll in the palisade); at least some leaves turning bright red in autumn; flowers with the outside of the calyx lobes usually tinged reddish purple; mature fruits usually partly or completely tinged pink to dark red (rarely in *C. erythrophyllum*); secondary xylem of older stems with islands of interxylary phloem (Verhoeven 1969; Verhoeven & Van der Schijff 1973).

All the species are closely related and specific limits within the section have been rather uncertain in recent years. Some of the characters employed to distinguish between the species are summarized in Table 1 and discussed in more detail below.

a. Habit and habitat

C. kraussii is a tree which occurs either within or in the vicinity of mist belts and coastal forests. It is unique because it is the only tree species of *Combretum* in the FSA region largely confined to a forest habitat. In cultivation it is nevertheless fairly adaptable and even survives the cold dry winters on the Transvaal Highveld. Although plants grown in the latter region flower profusely, the setting of seeds is generally very poor.

C. caffrum and *C. erythrophyllum* are usually trees, often branched from the base and nearly always confined to the banks of streams and rivers. Although both species oc-

asionally occur along water courses in forest regions, their main distribution ranges are outside these areas. *C. erythrophyllum* shows a particularly wide range of tolerance towards climatic conditions. It has, for example, been recorded from areas with very diverse environmental conditions such as the moist frost-free coastal region of Natal on the one hand and the Transvaal Highveld with its dry, cold winters where frost occurs frequently on the other.

C. vendae and *C. nelsonii* are savanna species usually growing in a rocky habitat with sandy soils. Both are multistemmed shrubs, very rarely small trees.

The few specimens of *C. woodii* that I have seen in the field were definitely tree-like. The species has been recorded from both forest (especially in Swaziland) and savanna habitats. In cultivation *C. woodii* appears to be unable to adapt to conditions outside its range but where both *C. erythrophyllum* and *C. kraussii* are able to cope quite satisfactorily (Carr pers. comm.). According to Palmer & Pitman (1972) *C. woodii* is sometimes a woody forest climber. However, I am rather reluctant to accept this statement until more field observations of the species have been done. In this regard Carr (pers. comm.) has observed young plants of *C. woodii* where actively growing shoots occasionally coil, thereby suggesting that the species may sometimes act as a climber. Once Carr (pers. comm.) also observed a similar coiling of young shoots in a non-climbing species such as *C. molle*. I have encountered the same phenomenon in *C. kraussii* (also recorded on a sheet, Moll 1722, in PRE) but it is highly uncommon and obviously only a temporary event.

b. Foliage leaves

Herbarium specimens of section *Angustimarginata* are very often covered (at least in part) with a hard, shiny layer of glutinous secretion. The presence of such a layer is frequently indistinct in living material. This secretion is particularly conspicuous on the leaves and young fruits of *C. nelsonii*. In the herbarium sterile or fruiting specimens of *C. nelsonii* are reminiscent of *C. apiculatum* Sond. which is also characterized by copious glutinous secretions.

Leaf shape is variable but nevertheless useful to distinguish some species. *C. caffrum* can readily be separated by its glabrous, narrowly elliptic leaf blades. Leaves in the other species are usually elliptic, ovate or obovate with the apex more pointed in *C. erythrophyllum*. The leaves in *C. woodii* are relatively large (often up to 160 mm long, 75 mm wide) with the lamina tending to be longitudinally folded upward along the midrib and with the margin often conspicuously wavy.

Differences in the colour of the leaves have been noticed in the field. Leaves of *C. kraussii* and *C. vendae* are dark green (with a tinge of grey in the latter) but usually light or medium green in the other species. This difference in colour is particularly conspicuous in areas where the distributions of *C. kraussii* and *C. erythrophyllum* overlap.

For additional leaf characters of taxonomic importance see 5.1c and 5.3.

c. Indumentum

The indumentum in *Combretum* consists of unicellular

Table 1 Summary of salient differences between the species of *Combretum* section *Angustimarginata*

	<i>C. kraussii</i>	<i>C. woodii</i>	<i>C. erythrophyllum</i>	<i>C. caffrum</i>	<i>C. nelsonii</i>	<i>C. vendae</i>
Geographical distribution	eastern parts of southern Africa	south-eastern Transvaal, Swaziland and northern Natal	widespread in eastern and central parts of southern Africa	eastern Cape, Ciskei and Transkei	central parts of Transvaal	central parts of Venda
Habitat	nearly always in or near forests	savanna, occasionally forest	nearly always along the banks of watercourses or near water		savanna, usually rocky terrain with sandy soils	
Habit	tree	tree, shrub or climber (?)	tree		usually shrubs, rarely small trees	
Leaves (mature and fresh)						
Shape	elliptic or obovate-elliptic	broadly elliptic, ovate-elliptic or ovate, rarely obovate-elliptic	elliptic to oblong elliptic	narrowly elliptic or lanceolate	elliptic, obovate-elliptic or obovate	
Colour (adaxial)	dark green	light to dark green	light to medium green, very rarely dark green			dark greyish green
Margin & folding of lamina	often slightly wavy, lamina occasionally slightly twisted	usually conspicuously wavy with lamina longitudinally folded upward along the midrib	occasionally slightly wavy, lamina often slightly twisted			
Lamina surface (abaxial)	glabrous (except for scales)		distinctly hairy, at least on the midrib and secondary veins; very rarely glabrous	glabrous (except for scales)		densely tomentose, very rarely almost glabrous
Intersecondary veins (abaxial)	more or less plane	conspicuously raised	raised	more or less plane		conspicuously raised
Reticulation (abaxial)		plane or slightly raised				
Scales (number of radial walls)	8(10)	8(10)–16				
Inflorescences	elongated spikes, (25)35–60(85) mm long		subcapitate spikes, (10)15–20(35) mm long			
Flowers						
Shape of upper receptacle	cupuliform; flat, slightly concave or convex at the base		more or less campanulate	cupuliform; flat or slightly convex at the base	usually clearly divided into a more or less campanulate lower part containing the disk and an expanded upper part which is more or less cupuliform	
Surface of lower receptacle	glabrous (except for scales) or very sparsely pubescent		densely pubescent	glabrous (except for scales) or very sparsely pubescent		densely pubescent
Pedicels	occasionally present, up to 1 mm long	absent				
Colour of mature fruits	usually partly or completely tinged pink to dark red		yellowish green, rarely tinged pink	usually partly or completely tinged pink to dark red		

compartmented trichomes (combretaceous hairs) and glandular peltate trichomes (scales). The present study has shown that characters of the indumentum are useful to distinguish between the species. With regard to the combretaceous hairs, mature leaves of *C. kraussii*, *C. nelsonii*, *C. woodii* (see note under 5.3) and *C. caffrum* are glabrous (or almost so) while those of *C. erythrophyllum* are nearly always hairy, but not as densely as *C. vendae*. In addition the rachis of the inflorescence is nearly always rather densely pubescent in all the species. In fresh material the hairs are greyish in *C. vendae* and white in the other species. Hair colour in the latter species gradually changes to brown or reddish brown in herbarium specimens. After four years no colour change has yet been noticed in herbarium specimens of *C. vendae*. It may, however, take more than ten years for the change to be noticeable.

The structure of the scales has proved to be an extremely valuable source of diagnostic characters on mainly sectional and occasionally specific level. This has been admirably demonstrated mainly by C.A. Stace in a series of papers (e.g. Stace 1961, 1965, 1969, 1980 & 1981). It was therefore not surprising when the structure of the scales provided the first clue to the taxonomic affinities of *C. vendae*.

According to Stace (1969) section *Angustimarginata* is characterized by scales *ca.* 50 – 75 μm diam.; outline circular, not scalloped with the cell-plate delimited by 8 – 16 primary radial walls alone. I have studied scales from all the species of the section and the results, on the whole, confirmed the observations of Stace as well as those of other workers (Verhoeven 1969; Verhoeven & Van der Schijff 1973).

C. kraussii is clearly distinct with the scales nearly always divided by eight, rarely up to 10, radial walls. In all the other species the scales are divided by 10 – 16, very rarely as few as eight, radial walls.

In the literature the structure of the scales is depicted as more or less circular with the cell walls clearly distinguishable. However, I have found it rather difficult to ascertain the number of radial walls in the majority of specimens examined. The scales on mature leaves from both herbarium specimens and spirit material are usually shrivelled to some degree and very often apparently dead (at least without visible cell contents). Scales from very young leaves (unfortunately not always present on herbarium specimens) show the scale features the clearest.

Scales of *C. vendae* are shown in Figure 3. The scales of this species are rather irregularly outlined, occasionally with some radial cells not reaching the centre. This is somewhat reminiscent of the scales illustrated for sections *Chionanthoidea* Engl. & Diels and *Polyneuron* Exell by Stace (1969). The scale drawings for section *Angustimarginata* by Stace (1969) unfortunately tend to be semi-diagrammatic. Those supplied by Verhoeven (1969) (also presented in Verhoeven & Van der Schijff 1973) are more realistic and agree with the pattern in *C. vendae*.

In *Combretum* the evolutionary pathways that the structure of the scales has followed, are obscure (Stace 1969). The simplest type of scale consists of eight radially arranged cells. According to Stace there is evidence that all or most scales of more complex construction pass through the eight-celled stage during development. Although the eight-celled scales of *C. kraussii* could be argued as a case of neotony and

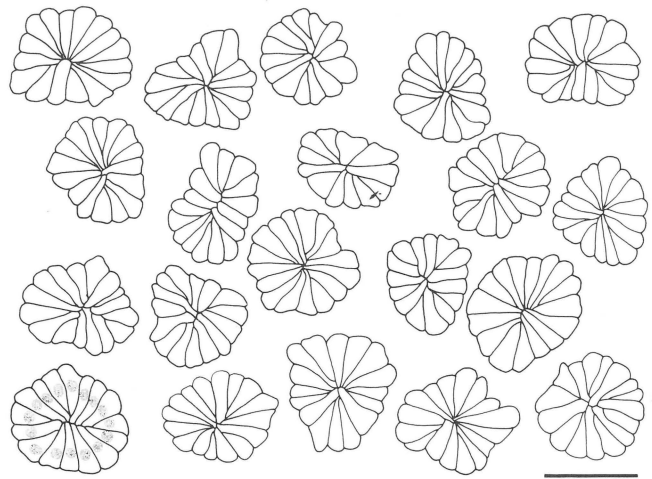


Figure 3 *Combretum vendae*. Selection of glandular scales from the upper lamina surface of a single leaf (obtained from leaf scrapings). Only cellular delimitation is shown with one scale indicating the position of the nuclei (Van Wyk & Theron 4923). All surface views. Bar = 50 μm .

therefore a derived condition, this seems unlikely considering other correlated ancestral characters. I have consequently assumed that the eight-celled scales of *C. kraussii* represent the primitive condition from which the usually 10 – 16-celled scales of the other species have been derived.

d. Inflorescences

The inflorescences in section *Angustimarginata* are axillary spikes. These are rarely arranged in short pseudo-panicles owing to the suppression of leaves on the new season's flowering shoots. A possible evolutionary tendency in the *Combretaceae* is the congestion of the flowers in densely flowered spikes or racemes (Exell 1954).

On the basis of inflorescence length, section *Angustimarginata* can be divided into two groups of species. *C. kraussii* and *C. woodii* are nearly always characterized by elongated spikes (25)35 – 60(85) mm long and with the axis rather laxly flowered. In the other species the inflorescences are nearly always congested into subcapitate spikes (10)15 – 20(35) mm long.

e. Flowers

Besides the structure of the scales, perhaps the most conspicuous taxonomic feature in *Combretum* is the shape of the upper receptacle (hypanthium). One of the main evolutionary tendencies postulated for the *Combretaceae* is a gradual elongation of the upper receptacle, especially noticeable in *Combretum* (Exell 1954). For example, the upper receptacle in section *Hypocrateropsis* Engl. & Diels is slightly developed and almost flat. This section may be regarded as primitive. It was placed by Engler & Diels (1899) at the beginning of their system, followed by sections showing a progressive increase in the length of the upper receptacle.

A comparison of the flowers in section *Angustimarginata* has revealed conspicuous differences between the species. Most of my observations are based on spirit material which is more reliable for determining the shape of the upper receptacle. A 'typical' flower for five of the six species

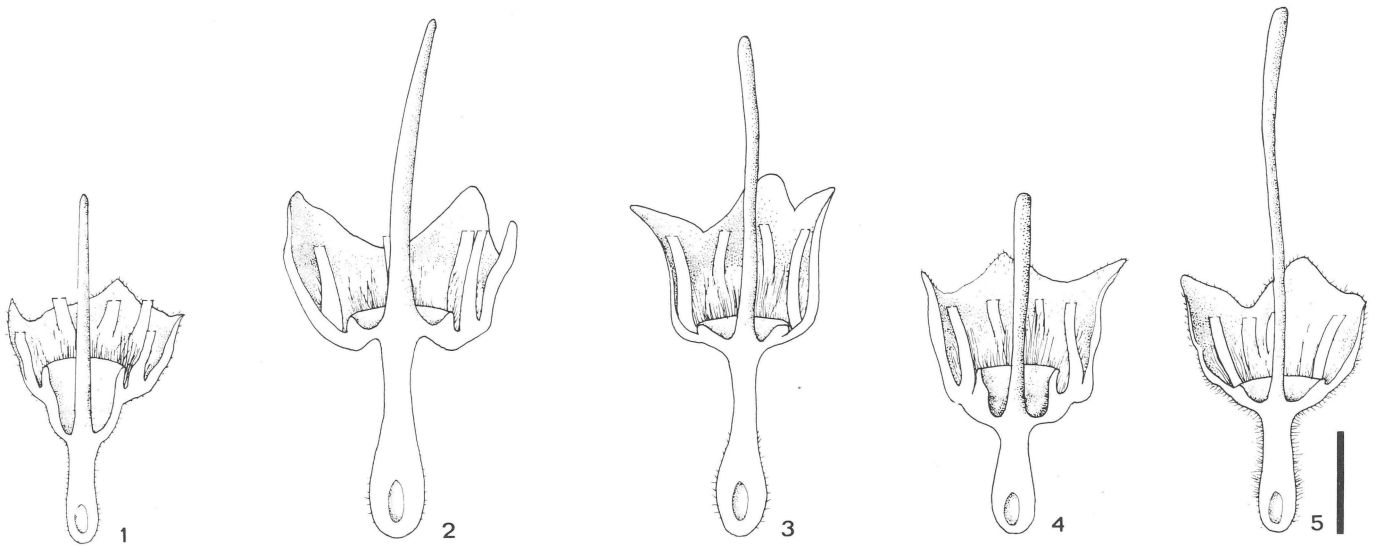


Figure 4 Comparison between flowers of species of *Combretum* section *Angustimarginata* (longitudinal sections not showing petals, stamens and hairs on inner surface of sepals). 1. *C. vendae* (Van Wyk & Theron 4923); 2. *C. kraussii* (Van Wyk 5895); 3. *C. caffrum* (Van Wyk & Kok 5030); 4. *C. nelsonii* (Van Wyk 5756); 5. *C. erythrophyllum* (Van Wyk & Kok 5776). Bar = 2 mm.

is shown in Figure 4. The excellent drawings in Engler & Diels (1899) also clearly show the floral differences between *C. kraussii* (Plate VIIIA) and *C. erythrophyllum* (Plate VIIB, C & D; = *C. lydenburgianum* Engl. & Diels and *C. glomeruliflorum* Sond.). Unfortunately spirit-preserved floral material of *C. woodii* was not available for study.

C. kraussii is once again distinct because it has flowers with the upper receptacle cupuliform and flat or slightly concave at the base. The lower receptacle is relatively long and slender with the part between the inferior ovary and upper receptacle well developed. A very short pedicel (up to 1.0 mm long) is occasionally present at the base of the lower receptacle (not shown in the drawing). I regard this as a primitive feature. It has not been observed in any of the other species.

The flowers of *C. caffrum* show some resemblance to those of *C. kraussii* in the shape of the upper and length of the lower receptacle. However, the base of the upper receptacle is very rarely concave and tends to be slightly convex in the former species. In both species the lower receptacle can be glabrous (except for scales) or very sparingly pubescent.

The flowers of *C. erythrophyllum* are densely pubescent on the outside (especially the relatively short lower receptacle) and the shape of the upper receptacle is more or less campanulate.

Floral features are rather similar in *C. vendae* and *C. nelsonii*. A conspicuous feature is the more elongated upper receptacle which is visibly divided into two regions, viz. a lower more or less campanulate or even tubular part containing the disk and an expanded upper part which is more or less cupuliform. The lower part is particularly well developed in *C. vendae*. On account of the more elongated upper receptacles I have assumed that the flowers of *C. nelsonii* and *C. vendae* are the most specialized in the section. The lower receptacle is densely pubescent in *C. vendae* and almost glabrous or sparsely pubescent in *C. nelsonii*.

Limited flowering material of *C. woodii* was available and

then from herbarium specimens only. The morphology of these flowers is very similar to that of *C. kraussii*.

5.2 Species delimitation and interspecific relationships

Within section *Angustimarginata*, I regard *C. kraussii* as the most primitive species. As has been shown above, this view is supported by evidence derived from the morphology of the scales, inflorescences, flowers as well as its habit and preference of habitat. The geographical distributions of the other species all come close to, or even partly overlap with, that of *C. kraussii*. Therefore I suggest that each of these species probably originated independently of *C. kraussii*. These derived species could be the result of mainly climatic and habitat selection and represent adaptations to the more mesic and even xeric environmental conditions outside the forest environment.

C. caffrum and *C. erythrophyllum* were not very successful in adapting to drier soil conditions and are therefore still bound to watercourses where subsurface water is readily available most of the year. *C. caffrum* is mainly restricted in distribution to the eastern Cape, Ciskei and southern parts of Transkei. *C. erythrophyllum* is a widespread and more adaptable species (see also 5.1 a). However, its distribution barely overlaps with that of the former species.

C. nelsonii, *C. vendae* and *C. woodii* may represent independent adaptations to relatively drier savanna conditions, each restricted to a different geographical area viz. *C. nelsonii* in the central Transvaal, *C. vendae* in the central mountainous region of Venda and *C. woodii* in the south-eastern Transvaal, Swaziland and north-eastern part of Natal. *C. woodii* is the only one of the three species which occurs in both savanna and forest regions. The shrubby habit of *C. nelsonii* and maybe *C. vendae* is probably an adaptation to fire. The effect of bush fires on the evolution of *Combretum* in Africa is discussed in more detail by Exell & Stace (1972).

There is some evidence suggesting that the morphological discontinuity between *C. kraussii* and some of its sibling species is not yet complete. Very rarely, herbarium specimens

which seem to be intermediates between *C. nelsonii*, *C. woodii* and *C. kraussii* are found. However, I believe that many, if not all of these 'aberrant' specimens could be assigned to one of the existing species if the populations of plants from which they come are examined in the field.

A shrubby species of *Combretum* (of which I have seen only fruiting material) from the western Soutpansberg mountains and the Blouberg does create some difficulties. These specimens are obviously closely related to *C. kraussii* and appear to be yet another adaptation to savanna conditions. Although vegetatively also very similar to *C. nelsonii* (which in my view does not occur in the Soutpansberg area), I suggest that the resemblances may be due to convergence. A peculiarity of the Soutpansberg plants is the prominently raised venation on the lower surface of the leaf blade which is found mainly in plants growing under xeric conditions (such as extremely rocky terrain). Plants from the same population but in deeper soil have a more or less planar venation. A similar local variation in venation has not yet been observed in *C. nelsonii*. The colour of the mature leaves in the Soutpansberg plants is often a glaucous green, unlike the light green of typical *C. nelsonii*. For the present I retain these plants in *C. kraussii* with reserve, although subspecific rank should perhaps be considered for them. However, if in future the specimens are referred to *C. nelsonii* (when the flowers are better known), the question of a polytopic origin for the latter species should be considered. Exell (1968) grouped some of the specimens from the Blouberg with specimens which I would refer to *C. nelsonii* and described them as a hybrid between *C. erythrophyllum* and *C. kraussii* — a view with which I do not agree.

Exell (1970, 1978) included *C. nelsonii* and *C. woodii* in the synonymy of *C. kraussii*. In my experience *C. nelsonii* is clearly distinguishable in the field and it should be maintained. According to Verhoeven (1969) the anatomy of the leaf and structure of the scales support the distinction between *C. nelsonii* and *C. kraussii*. *C. woodii* was described by Dümmer (1913) and based on the specimens Wood 522 from Durban and Galpin 1176 from Barberton. I have only seen the latter syntype and am satisfied that it represents a distinct species. Although I have not seen the former syntype, the locality suggests that it is most probably a specimen of *C. kraussii*. I must therefore stress the fact that my concept of *C. woodii* is provisionally based only on Galpin's collection. Excellent colour photographs of 'typical' *C. woodii* are provided by Van Wyk (1974).

The name, *C. woodii*, has frequently been misapplied in southern African herbaria. Many specimens previously distributed under this name are in fact *C. kraussii*. *C. woodii* is probably the least known species of the section and much more field work is needed to clarify its relationship with especially *C. kraussii* to which it is very closely related (also see comments under 5.3).

Both Stace (1969) and Exell (1970, 1978) hint that *C. caffrum* (= *C. salicifolium* E. Mey.) may be no more than a narrow-leaved variation (subspecies or variety according to the former author) of *C. erythrophyllum*. Besides the resemblance in habitat, field observations provide little support for such a treatment. In my opinion *C. caffrum* is rather more closely related to *C. kraussii* than to *C. erythrophyllum*, especially if the floral morphology is com-

pared.

A final point to be considered relates to the question of whether specific or subspecific rank should be applied to the principal taxa of section *Angustimarginata*. This question applies particularly to *C. vendae*. A noteworthy feature of *Combretum* in Africa is the occurrence of pairs of species which differ markedly in indumentum and sometimes venation characters, but apparently scarcely at all in other structural features. Whereas some authors regarded each form as a distinct species, others treated both as a single combined species. However, the tendency in recent years has been to treat both forms as subspecies provided that variation is largely discontinuous. See for example the subspecies of *C. collinum* Fresen. (Okafor 1967), *C. celastroides* Welw. ex Laws. (Exell 1968, 1978), *C. apiculatum* Sond. and *C. psidioides* Welw. (Exell 1961, 1970, 1978).

Should *C. vendae*, in the light of the above, not be treated as a hairy subspecies of *C. nelsonii* or perhaps *C. kraussii*? To this my answer is 'no', because I do not think a situation similar to those mentioned in the examples above, applies. Both hairy and almost glabrous forms occur in *C. vendae*, although the former is the predominant state. A similar variation has also been observed in *C. erythrophyllum*, *C. kraussii*, *C. caffrum* and probably in *C. woodii* (see 5.3), each time with one of the two character states completely dominating the other in its frequency of expression.

Whether or not to take a lumpers' approach and consider section *Angustimarginata* as a single aggregate species with a series of subspecies is probably a matter of personal choice. Judged by the species names and remarks on the herbarium specimens examined, it is evident that an overwhelming majority of specimens (*C. woodii* being a notable exception) have been correctly classified according to the species maintained in the present paper. There is little doubt that the treatment proposed for section *Angustimarginata* is workable in the field and with some experience also in the herbarium. To accept subspecies on the basis of the relatively rare odd herbarium specimens is undesirable and obviously not in the interests of nomenclatural stability.

5.3 Key to the species of *Combretum* section *Angustimarginata*

In the following key no provision is made for variations which are very rare (e.g. almost glabrous specimens of *C. vendae* or slightly hairy specimens of *C. kraussii*) and therefore unlikely to be encountered. The leaves of *C. woodii* are taken as glabrous but more fieldwork is needed to confirm whether this is always the case. A number of specimens which may belong to this species, but which have hairy leaves, have been encountered in PRE (See Appendix). Pending further study, no provision is made in the key for those specimens of uncertain identity (see 5.2) from the western Soutpansberg and the Blouberg. Because most of the species are confined to a well defined geographical area and/or habitat, this information is of considerable aid in identification and has therefore been incorporated in the key. However, some experience with the group may be essential to identify aberrant and sterile specimens. To help convey my concept of the taxa to future students, a selection of representative specimens is supplied in the Appendix.

Key to the species of *Combretum* section *Angustimarginata*

1. Leaves glabrous beneath when mature (except for scales), often with hair-tuft domatia:
 2. Flowers in elongated, rather laxly flowered spikes, (25)35 – 60(85) mm long; plants occurring both in forest and savanna regions:
 3. Leaf lower surface with secondary veins raised but intersecondary veins \pm plane; scales composed of 8(– 10) radial cells; trees; nearly always occurring in or near forests; widespread *C. kraussii*
 3. Leaf lower surface with both secondary and intersecondary veins conspicuously raised (often yellowish in dried specimens); scales composed of (10–) 16 radial cells; trees, shrubs or climbers(?); occurring in forest and savanna regions; recorded from the south-eastern Transvaal, Swaziland and northern Natal *C. woodii*
 2. Flowers in rather congested subcapitate spikes, (10)15 – 20(35) mm long; plants associated with savanna or if in forest regions then confined to gallery bush:
 4. Leaves elliptic, obovate-elliptic or obovate; flowers with the upper receptacle visibly divided into a lower \pm campanulate part containing the disk and an expanded \pm cupuliform upper part; usually shrubs; recorded from savanna on rocky terrain in central Transvaal *C. nelsonii*
 4. Leaves narrowly elliptic or lanceolate; flowers with the upper receptacle \pm cupuliform, not visibly divided into a lower and upper part; usually trees; recorded from the banks of watercourses in the eastern Cape, Ciskei and Transkei *C. caffrum*
1. Leaves distinctly hairy beneath when mature, at least on the midrib and secondary veins:
 5. Flowers with the upper receptacle visibly divided into a lower \pm campanulate part containing the disk and an expanded \pm cupuliform upper part; reticulation of under surface of lamina conspicuously raised; recorded only from Venda *C. vendae*
 5. Flowers with the upper receptacle \pm campanulate, not visibly divided into two parts; reticulation of under surface of lamina plane or slightly raised; widespread along watercourses in southern Africa *C. erythrophyllum*

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Appendix Selection of representative specimens. All specimens are housed in the National Herbarium (PRE), Pretoria.

- A. Clear-cut species upheld in this paper:
1. *Combretum caffrum*: Bayliss 1134; Rogers 12019; Strey 11191; Van Wyk & Kok 5830, 5849; Wells 3587.
 2. *C. erythrophyllum*: Burt-Davy 2328; Codd 4390; Coetzee 614; Hardy 1926; Hemm 265; Mogg 30578; Moll 1062; Strey 8431; Theron 1528.
 3. *C. kraussii*: Killick 203; Kluge 307; Mohle 457; Moll 4566; Scheepers 753; Strey 9289, 11028; Van Wyk 2177; Van Wyk & Kok 5787.
 4. *C. nelsonii*: Carr 206; Codd 7049; Coetzee 1195; Galpin 11693; Schlieben 9186; Van Wyk 5755, 5757, 6019.
 5. *C. vendae*: See under 4 in text.
 6. *C. woodii*: Codd 10291; Culverwell 654, 955; Kemp 758, 875; Nell 237; Van der Schijff 10291; Ward 2130.

B. Taxa of doubtful identity:

1. Specimens from the western Soutpansberg and the Blouberg which show affinity to *C. kraussii* and *C. nelsonii*: Burger 357; Codd 8704; Codd & Dyer 9132; Van Wyk 5537, 5550, 5557, 5559.
2. Specimens with hairy leaves from the same geographical area as *C. woodii*, with which it may be conspecific: Acocks 12985; Codd 1904; Kemp 991.

Short Communication

Variation of the optical properties during leaf development of *Ochna pulchra*

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The changes in the absorption of solar radiation by leaves of *Ochna pulchra* during leaf expansion were investigated. The observed differences are small and cannot result in significantly different leaf temperatures.

Die verandering in the absorpsie van sonstralingsenergie deur blare van *Ochna pulchra* tydens blaarvergroting is ondersoek. Die waargenome veranderinge is klein en kan nie tot noemenswaardige verskille in blaarteratuur aanleiding gee nie.

Keywords: Leaf temperature, *Ochna pulchra*, optical properties

A recent investigation of shoot growth of *Ochna pulchra* Hook. by Rutherford & Panagos (1982) showed that the period of maximum shoot expansion corresponds with the period when leaf temperatures are highest. It is well known that leaf temperature depends largely on the amount of absorbed solar radiation and thus on the optical properties of the leaf. During leaf expansion of *Ochna pulchra* a marked change in leaf colouration occurs. Young leaves are first copper red, then turn yellowish olive, green olive and finally dark green. Bate & Ludlow (1978) suggested that the anthocyanins in young leaves might protect nuclear DNA during leaf tissue differentiation. Changes in the optical properties in the visible range of wavelengths (400 to 750 nm) very often lead one to believe that an equally large change in the absorption of solar radiation must result, giving rise to significantly different leaf temperatures. In the case of *Ochna pulchra* this could mean that the dark copper red colouration of the immature leaves might result in them

attaining a considerably higher temperature during the day than if they were green and the rapid growth of the young leaves could be a consequence of this high temperature.

However, only about 52 % of the global radiation that is incident on a leaf at about noon (clear sky) is visible radiation, the rest being infrared (42 %) and ultraviolet (6 %) radiation with wavelengths from 750 to 3000 nm and 300 to 400 nm respectively (Eller & Grobbelaar 1982). Consequently an investigation into whether a major change in colouration is paralleled by an equally large variation of the absorbed solar energy has to include the determination of the optical properties in both the visible and the infrared wave ranges.

During a detailed investigation of the optical properties of mature leaves of woody species of the Sourish Mixed Bushveld (Eller *et al.* 1984) some additional measurements were made of expanding leaves of *Ochna pulchra*. The optical properties of the leaves were determined with an ISCO SR spectroradiometer (Instrumentation Specialities, Lincoln) with an integrating sphere as described by Eller (1972). Measurements were taken over the wavelength range from 400 to 1350 nm. This wavelength range was extended to 300 and 3000 nm by an approximation as described by Eller *et al.* (1984).

Figure 1 compares the absorptivities of expanding *Ochna pulchra* leaves at different growth stages with those of a mature leaf. The general pattern of the values for the mature leaf is that of a typical green and slightly sclerophyllous leaf, with high values in the visible and low values in the shortwave infrared. In the visible region of the spectrum immature leaves show differences corresponding to their colouration but all leaves have about the same absorptivities in the infrared (750 to 1350 nm). In this wave range and also in the longer wavelength region of the visible spectrum, mature leaves generally have higher absorptivities than young leaves. This is a result of the more sclerophyllous nature of the old leaves.

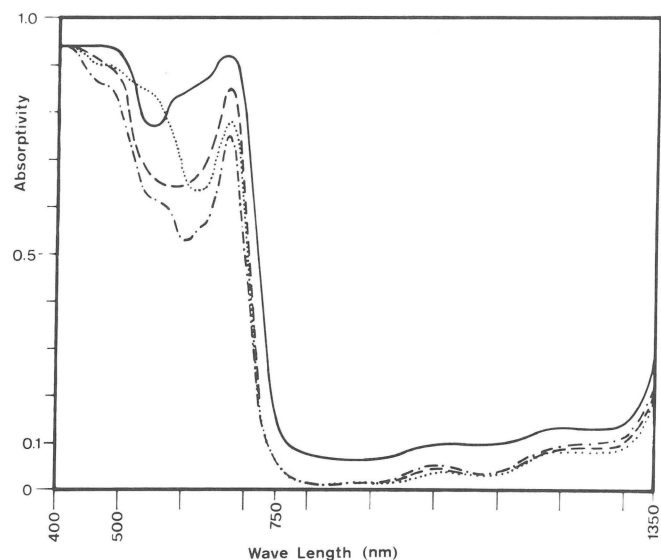


Figure 1 Spectral absorptivities of *Ochna pulchra* leaves. copper red young leaf; - . - . - yellow olive intermediate leaf; - - - - green olive intermediate leaf; ——— green mature leaf.

Table 1 gives values for reflectance, transmittance and