

# The taxonomy, chorology and reproductive biology of southern African Meliaceae and Ptaeroxylaceae

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## ABSTRACT

Information is provided on the taxonomy, chorology and reproductive biology of 14 indigenous and two introduced species of Meliaceae in southern Africa, and on *Ptaeroxylon* (Ptaeroxylaceae). Two new taxa are described: *Nymanieae* F. White, tribus nov. and *Turraea streyi* F. White & B. T. Styles, sp. nov. *Nurmonia* (Harms) F. White, comb. et stat. nov., a new section of *Turraea* L. is created. The account complements the treatments of these families in the *Flora of southern Africa*.

## UITTREKSEL

Inligting word verskaf oor die taksonomie, chorologie en voortplantingsbiologie van 14 inheemse en twee ingevoerde spesies van Meliaceae in suidelike Afrika en oor *Ptaeroxylon* (Ptaeroxylaceae). Twee nuwe taksons word beskryf: *Nymanieae* F. White, tribus nov. en *Turraea streyi* F. White & B. T. Styles, sp. nov. *Nurmonia* (Harms) F. White, comb. et stat. nov., 'n nuwe seksie van *Turraea* L. word geskep. Hierdie verslag is aanvullend tot die behandelings van hierdie families in die *Flora of southern Africa*.

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## INTRODUCTION

This paper should be read in conjunction with the accounts of Meliaceae and Ptaeroxylaceae in the *Flora of southern Africa* (White & Styles, in press, a & b). In the latter, descriptions are brief and little ancillary information is provided. In the present account three new taxa (the tribe Nymanieae, the section *Nurmonia* of *Turraea* and the species *Turraea streyi*) are described. Reasons are given for the taxonomic decisions on which the flora accounts are based. The geographical patterns of variation in *Ekebergia capensis* and *Turraea obtusifolia* are analysed and evaluated. The two southern African species of *Trichilia*, *T. dregeana* and *T. emetica*, have a complex and confused taxonomic and nomenclatural history. This is unravelled at some length.

In its ecology the Meliaceae is more diverse than most tropical families of comparable size, particularly with regard to pollination and dispersal. This is also true for the subtropical, southern African members. What little is known about this subject is briefly described under each species, and suggestions are made for further work.

In the discussion at the end of the paper the southern African Meliaceae are used to illustrate certain themes of general biological interest — in particular

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the contributions that chemistry and field ecology can provide. Some comments are also made on the methods of taxonomic research. The fact that taxonomy is basically a visual art is emphasized.

In the descriptions the term aril is used in an ecological rather than in a precise anatomical sense; minor variation in the number of floral parts is ignored.

#### GENERIC AND FAMILY DELIMITATION

For its size the Meliaceae probably contains a wider range of floral and fruit structures than any comparable group (White in Pennington & Styles 1975: 419). It is also diverse in vegetative morphology. Diversity of the flower and fruit is related to the wide variety of pollen vectors and agents of dispersal, though, with only a few exceptions (e.g. Pannell & Koziol, in press), this has been little studied.

Comparative studies within the family indicate that it has retained a primitive type of fruit, in this case a capsule with brightly coloured, bird-dispersed, arillate seeds, and that all other fruit types in the family are derived (Pannell & White 1985: 1). Primitive fruits persist alongside the advanced and this provides clues to the pathways of evolutionary change. The situation is similar for the meliaceous flower.

Persistence, or lack of extinction of the kind found in Meliaceae, poses taxonomic problems. It has given rise to some extremely variable groups which are difficult to define taxonomically, especially when the function of the characters used in classification is not understood.

Because of the nature of its variation pattern, the Meliaceae has had a long history of taxonomic instability, succinctly described by Pennington (in Pennington & Styles 1975). He gives special consideration to genera whose inclusion in the family has been controversial. Among them, he concludes that *Nymania* belongs to Meliaceae, but, following Leroy (1959, 1960) and White & Styles (1963, 1966), that *Ptaeroxylon* should be removed from that family. In general, Pennington's views have been followed, but in some publications (e.g. Airy Shaw 1966, 1973; Dyer 1975) *Nymania* is excluded and *Ptaeroxylon* (Dyer 1975) retained. More recent data especially from phytochemistry, support Pennington's conclusions.

The Meliaceae is poorly represented in southern Africa. It is therefore difficult, in a purely local context, to assess the relationships of anomalous genera such as those mentioned above. For that reason the evidence for including the one genus and not the other is summarized below. Two South African species of *Turraea* occupy an isolated position within it, and their relationships are also discussed.

#### The position of *Ptaeroxylon*

Since *Ptaeroxylon* was first described (Ecklon & Zeyher 1834–35), its taxonomic position has been uncertain. In their protologue, the original authors suggest that its true affinities may be with Rutaceae, but they tentatively grouped it with Sapindaceae 'un-

til such time as it could be studied by more experienced botanists'.

As long ago as 1860, Sonder (1860: 242), placed it immediately after Sapindaceae as a genus of uncertain affinity, and indirectly indicated that it might qualify for family rank. According to Leroy (1960), Sonder's name 'Ptaeroxyleae' should be regarded as a *nomen provisorium*, though Airy Shaw (1966, 1973) cites Sonder as the legitimate author of Ptaeroxylaceae. Leroy, who had elsewhere (1959) discussed the taxonomy of *Ptaeroxylon* together with the Malagasy genus *Cedrelopsis* Baillon, concluded that, in their morphology, secondary xylem and pollen, these genera are so distinct that family rank, which he formally proposed, is required. White & Styles (1966), partly using evidence from an unpublished thesis (Jenkin 1961), independently reached a similar conclusion.

During the hundred years between 1860 and 1960 *Ptaeroxylon* was usually placed, sometimes with reservations, either in Sapindaceae (Hooker 1862; Phillips 1921; Mauritson 1936) or Meliaceae (Radlkofer 1890; Harms 1896, 1940; Phillips 1951), where Dyer (1975) allowed it to remain.

In a comprehensive review of all the evidence then available, Pennington & Styles (1975) showed that *Ptaeroxylon* and *Cedrelopsis* share a few features with Meliaceae, Rutaceae and Sapindaceae, but are so different in other respects that the family Ptaeroxylaceae should be retained.

According to Taylor (1983; see also Dean & Taylor 1966) *Ptaeroxylon* and *Cedrelopsis* are sufficiently distinct in their chemistry to form a separate family. Limonoids, a group of oxidized triterpenes which occur in Rutaceae, Meliaceae, Cneoraceae and in *Harrisonia abyssinica* (Simaroubaceae), are unknown in Ptaeroxylaceae. However, absence may not be very significant. What is much more important is that Ptaeroxylaceae does contain many other unusual compounds not found in any Meliaceae, most notably chromones of the ptaeroxylin group. These substances otherwise have been found only in Cneoraceae and in *Spathelia* and *Harrisonia* (Simaroubaceae). The former is usually placed in Rutaceae though some botanists think it would be better accommodated in Simaroubaceae.

#### The position of *Nymania*

*Nymania*, in its fasciculate, linear, sclerophyllous leaves, almost free staminal filaments and large inflated capsules, is so different in appearance from other southern African Meliaceae that it is not surprising that some botanists who were concerned primarily with the flora of South Africa should have been tempted to exclude it from that family (Sonder 1860; Dyer 1975). Recent specialists of the Meliaceae, however, have been virtually unanimous on its inclusion, (e.g. Harms 1940; Pennington & Styles 1975), following the lead of Antoine Laurent de Jussieu (1789) and Ventenat (1799). Adrien de Jussieu (1830), however, in his early monograph of the family, was unsure of its affinity, and mentioned that a correspondent, M. Gay, thought it to be close to Sapindaceae.

Some authors of general systems of classification of flowering plants, who lacked detailed knowledge of the group, have, however, placed *Nymania* (or its illegitimate synonym, *Aitonia*, see below) in other families, including Sapindaceae (tribe Dodonaceae, Hooker 1862), or have suggested family rank (Airy Shaw in Willis 1966, 1973) as Aitoniaceae. One has expressed doubt concerning its systematic position (Sonder 1860).

Radlkofer (1890), the great authority on Sapindaceae, discusses the affinity of *Nymania* at some length and concludes that a relationship with the Meliaceae is very close. The resemblance between the fruit of *Nymania* and that of *Melanthus* (Meliaceae, a satellite of Sapindaceae) or *Dodonaea* was shown to be superficial. Many other characters, notably the 4-merous flowers, antisepalous position of the carpels, endospermous seed, curved embryo and intra-staminal disk, would not exclude it from the Meliaceae. Radlkofer notes in particular, that the continuous ring of sclerenchymatous tissue, which is present in the bark of the twigs of Sapindaceae, is absent from *Nymania* as in all other Meliaceae.

Pennington (in Pennington & Styles 1975) has studied *Nymania* in great detail in relation to all other genera of Meliaceae and to related families. He has shown that:

(1) most features of the pollen of *Nymania* are shared by members of the tribe *Turraeeae*;

(2) *Nymania* has secondary xylem which is very similar to that of *Calodectarya* and some species of *Turraea*, thus confirming its position in the Meliaceae, but it has other characters, namely the very small vessels and sparse or absent paratracheal parenchyma, found nowhere else in the family;

(3) in its foliage and seed structure, the Malagasy genus *Calodectarya* links *Nymania* to other Meliaceae.

In its chemistry, *Nymania* unequivocally belongs to the Meliaceae (Taylor 1983, 1984, pers. comm.; Maclachlan & Taylor 1982). Nearly every member of the family so far investigated has been found to contain one or more limonoids (p. 163). At the family level the chemotaxonomic distinctions are very clear. *Nymania* contains limonoids belonging to the Evodulone and Puriuranin groups. Those of the former are also found in species of *Carapa*, *Toona* and *Trichilia*, whereas the latter occur in *Aphananixis*, *Guarea*, *Toona* and *Trichilia*.

In conclusion there can be little doubt that the best place for *Nymania* is in the Meliaceae. Because of its isolation, however, tribal rank seems justified.

#### Tribus *Nymanieae*, tribus nova

*Meliaceae*: *Aitoniaceae* M. J. Roemer: 88 (1846), nom. illegit. (see p. 146).

*Aitoniaceae* Harvey: 243 (1860), nom. provis. et illegit.

*Aitoniaceae* Airy Shaw: xxi (1966), nom. illegit.

*Folia* simplicia, fasciculata, sclerophylla. *Sepala* 4. *Petala* 4. *Stamina* 8; filamenta solum basi coniuncta,

sine appendiculis; antherae medifixae. *Ovarium* 4-lobatum, loculis 4 praeditum. *Ovula* in loculo quoque bina, collateralia, parvo arillo carnoso ante seminis maturitatem fatisciente. *Semen* reniforme. *Embryo* valide curvata, tenui endospermio inclusa.

#### Typus tribus: *Nymania*

*Leaves* simple, fasciculate, sclerophyllous. *Sepals* 4. *Petals* 4. *Stamens* 8; filaments united only at the base, without appendages; anthers medifix. *Ovary* 4-lobed, with 4 locules. Ovules 2 in each locule, collateral, with a small fleshy aril which disintegrates before the seed reaches maturity. *Seed* reniform. *Embryo* strongly curved, embedded in thin endosperm.

#### The circumscription of *Turraea*

The majority of species of *Turraea* in tropical Africa have the following features:

simple leaves;

long and narrow, white or whitish petals;

an elongate staminal tube terminated by 10 or more appendages or a staminal frill;

an exerted style with an expanded style-head which is stigmatic only near the apex;

a loculicidal capsule containing reniform arillate seeds.

These characteristics are also found in some Malagasy and Far Eastern species.

There is evidence that in most species the flowers are fragrant at night and are pollinated by moths, though in some species, e.g. *T. fischeri* Gürke, birds may be responsible (White & Styles 1963: 307). It is possible that in most species the style-head functions as a pollen-presenter or *receptaculum pollinis*, though confirmation in the field is needed. The development of the aril varies greatly, though it is always relatively small, and it seems that the seeds, and sometimes parts of the capsule, are to some degree mimetic.

Certain species which are evidently closely related to *Turraea sens. strict.* lack one or more of its unifying features. Whether they should be included or not has sometimes been a matter of controversy. In certain cases the differences from typical *Turraea* appear to be related to different methods of pollination or dispersal, though in the absence of field studies this important subject will remain conjectural.

Pennington (in Pennington & Styles 1975: 446) has discussed the difficulty of generic delimitation in the Meliaceae, and advocates a pragmatic middle course between excessive lumping and excessive splitting, a case for each of which could be made on theoretical grounds.

In the subfamily Melioideae Pennington found that the majority of genera fall into four tribes (*Turraeeae*, *Trichilieae*, *Aglaieae* and *Guareeae*) which show a similar variation pattern. The majority of species in each tribe belong to a single genus, which, although it contains much variation, is still definable and cannot be satisfactorily split. The remaining species form a number of small satellite genera. In the *Turraeeae*, the satellite genera are as follows:

*Munronia* Wight, c. 10 species in India and Malasia; *Naregamia* Wight & Arn., 1 species in Angola, 1 species in India; *Humbertioturraea* J. F. Leroy, 3–4 species in Madagascar; *Calodecaryia* J. F. Leroy, 1–2 species in Madagascar; *Nymanina* Lindb., 1 species in southern Africa.

Pennington includes in *Turraea* certain species which form isolated groups within it; the latter appear to be less distinct than the satellite genera mentioned above. In this he partly follows Harms (1940) who demoted *Quivisia* Commers. ex Juss., *Calodryum* Desv. and *Grevellina* Baill. to sectional rank. Pennington also united with *Turraea* the monotypic genus *Nurmonia* Harms. based on the southern African *N. pulchella*, which Harms kept separate.

In revising Meliaceae for the *Flora of southern Africa* it was necessary to study *T. pulchella* alongside a new species, *T. streyi*, which is closely related to it and to reconsider the status of *Nurmonia*.

The isolated position of these two species in *Turraea* is confirmed. There are striking differences in the flowers and fruits which appear to be related to pollination and dispersal, and this may also be the case for other isolated groups within *Turraea*, e.g. *Quivisia*, and for some of the satellite genera.

It could be argued that the differences separating *T. pulchella* and *T. streyi* from typical *Turraea* are at least as great as those characterizing, say, the satellite genus *Naregamia*, and that *Nurmonia* should be restored to generic rank. In my opinion, in our present state of knowledge, such a view would be inadvisable. Until the biological significance of the distinguishing features of the satellite genera and anomalous species have been carefully studied and correctly interpreted, a generic re-assessment would serve little purpose. In the meantime, in order to focus attention on the problem and to emphasize the need for further study, especially in the field, the section *Nurmonia* is proposed below (p. 151) where its constituent species are described in as much detail as the rather sparse material allows.

#### NOTES ON INDIVIDUAL GENERA AND SPECIES

##### 1. NYMANIA Lindb.

*Nymanina* Lindb. in Notiser ur Sällskapet pro Fauna et Flora Fennica Förhandlingar 9: 290 (1868); Marloth: 112, 114, fig. 40d (1925); Harms: 94, fig. 24 (1940); Dyer: 299 (1975); Pennington & Styles: 460, fig. 4c (1975). Type species: *N. capensis* (Thunb.) Lindb.

*Aitonia* Thunb.: ('1776') 166, fig. 3 (1781); Thunb.: 52 (1782); Thunb.: 508 (1823); Sond.: 243 (1860); nom. illegit. non *Aytonia* J. R. & J. G. A. Forster (1776) Marchantiaceae).

*Aytonia* L.f.: 49, 303 (1781), emend. *Aitonia* p. 468.

*Carruthia* Kuntze: 141 (1891).

Marloth (1925) correctly observed that the genus *Aitonia* was named after William Aiton, gardener to King George III, and that *Aytonia* Thunb. 'is not valid as '*Aitonia*' Forst. (Marchantiaceae) was established in 1776'.

The name *Aitonia* Thunberg appears in most phanerogamic literature until the end of the nineteenth century, and Harms (1896) used it in his account of Meliaceae in *Die Natürlichen Pflanzenfamilien* though he adopted *Nymanina* in the *Nachträge* of that work (II:36, 1900). During the same period *Aytonia* Forster had also been popular among bryologists. In 1930, however, Schiffner proposed *Plagiochasma* Lehmann & Lindenberg (1832) as a *nomen conservandum versus Aytonia* of which he says 'descriptio omnino falsa' (Rehder in Rehder *et al.* 1935: 349–350), and this recommendation was subsequently adopted.

Rehder was unable to recommend that *Aitonia* Thunberg could be conserved and accepted *Nymanina* as the correct name for it. Most subsequent authors have concurred.

According to St. John (1971) the *Ayton* of the Forsters and the *Aiton* of Thunberg are two different individuals, but this view is untenable since Thunberg (1782) says 'in honorem Dom. Aiton, Hortulani in Horto Regio Kewensi' while Forster says 'Dedimus a Joanne Ayton — Hortulano primario Regis Magnae Britanniae in horto Botanico Kewensi'.

The title pages of the works in which *Aitonia* Thunberg and *Aytonia* Forster appear give the same date (1776), but according to Karsten (1946) Thunberg's protologue was not published until 1781. St. John (1971: 568) has also found evidence that the first edition of Forster's *Characteres* was published in 1775, but in a limited edition of six copies, only two of which survive.

In conclusion, *Aitonia* of Thunberg is illegitimate as are all taxa of higher rank based on it (Articles 18 and 32 of the current Code).

*Nymanina capensis* (Thunb.) Lindb. in Notiser ur Sällskapet pro Fauna et Flora Fennica Förhandlingar 9: 290 (1868). Type: South Africa, *Thunberg s.n.* (UPS, holo.).

*Aitonia capensis* Thunb.: 166 (1781).

##### *Distribution and Ecology*

*Nymanina capensis* is widely distributed within the Karoo-Namib floristic region of the Unesco/AET-FAT/UNSO Vegetation Map of Africa (White 1983a). It occupies two main areas separated by an interval of about 300 km.

In the north it extends southwards from Nauchas and Rehoboth in SWA/Namibia to near the mouth of the Orange River and from there inland to beyond the confluence of the Vaal and Orange Rivers. In the south it occurs in the Little Karoo and in similar and related vegetation further east.

Most of the localities from which *N. capensis* has been collected are located within mapping unit 51, Bushy Karoo-Namib shrubland, of White (1983a), which in South Africa consists largely of Acocks's (1975) three types of karroid broken veld, namely: No. 26, Karroid Broken Veld *sens. strict.*; No. 32, Orange River Broken Veld; No. 33, Namaqualand

Broken Veld, although *N. capensis* appears to be confined to the northern end of this.

North of the valley of the Orange River, *N. capensis* extends into the region of the southern Kalahari Sands (mapping unit 16, Kalahari Thornveld and Shrub Bushveld of Acocks, towards the southern limit of phytochorion XIV, the Kalahari-Highveld Regional Transition Zone of White). Here it occurs in bushland on the Langeberg and the Asbestos Mts and on the Kaap and Ghaap plateaux. On the lower slopes of the latter it is occasional all the way from Vryburg to Griquatown (A.A. Gubb *in litt.* 15 Feb. 1985). It also occurs on quite low, small and isolated, rocky outcrops emerging from a sea of red Kalahari Sand which extends for miles around, as in the vicinity of Pearson's Hunt, (2722 CC, Gubb *s.n.*).

In the south of its range, to the east of the Little Karoo *N. capensis* is mainly confined to dry areas in valleys and depressions in the rain shadow of mountain ranges, as far east as the Great Fish River between Carlisle Bridge and Komadagga (Mullins *s.n.*, 3326 AA). Some of these localities are inside the Tongaland-Pondoland Region (White 1983a) but near its extreme south-eastern limit.

Information on the vegetation types in which *N. capensis* occurs is given by Acocks (1975: 42, bushland on rocky soil in Veld Type 16, Kalahari Thornveld; 58, Veld Type 24, Noorsveld; 59, Veld Type 25, Spekboomveld; 61, Veld Type 26, Karroid Broken Veld of the Little Karoo; 72, Veld Type 32, Orange River Broken Veld; 75, Veld Type 33, Namaqualand Broken Veld), and by Van der Walt (1968), Noorsveld.

Figure 1 shows the overall distribution of *N. capensis* as revealed by herbarium specimens. A circle has been placed in the middle of each quarter degree square from which it is known to have been collected. In the north-western Cape, however, it is much more extensive than herbarium specimens in-

dicates. Site records in the area based on an outline distribution map and additional information supplied by A.A. Gubb are shown by stars.

Figure 2 shows that although *N. capensis* is widespread in the Cape Floristic Region it is absent from typical Cape vegetation and only occurs in enclaves of karroid types.

#### Pollination

According to Vogel (1954) birds visit the flowers, which, in the shape, size and colour of the corolla and in the structure of the androecium and copious nectar production, are typically ornithophilous.

#### Fruit type and seed dispersal

The fruits are large, loculicidal, papery capsules, up to 40 mm in diameter. They are deeply lobed with 4 laterally compressed, wing-like expansions. They are conspicuous and usually persist on the plant for several months. At first they are suffused with carmine, but later become straw-coloured and eventually silvery grey. The capsules are dehiscent only near the apex. Of the 8 ovules in the ovary, rarely more than 4 develop into seeds. In some herbarium specimens the seeds have fallen away from the placenta but in others they remain firmly attached.

The seeds are very distinctive. They are a dull dark brown and kidney-shaped, with a thick, rather woody, minutely puberulent testa. There is no aril, but in the ovule an adaxial concavity is filled by a fleshy outer layer of the testa which disintegrates before the seed is mature (Pennington & Styles 1975: 462). This leaves a deep chamber with a small entrance hole. The embryo is strongly curved and embedded in thin endosperm. The seeds appear to be much lighter than *Turraea* seeds of comparable size.

Little has been published on dispersal. Palmer & Pitman (1972: 1059) state that the capsules are dispersed by wind.

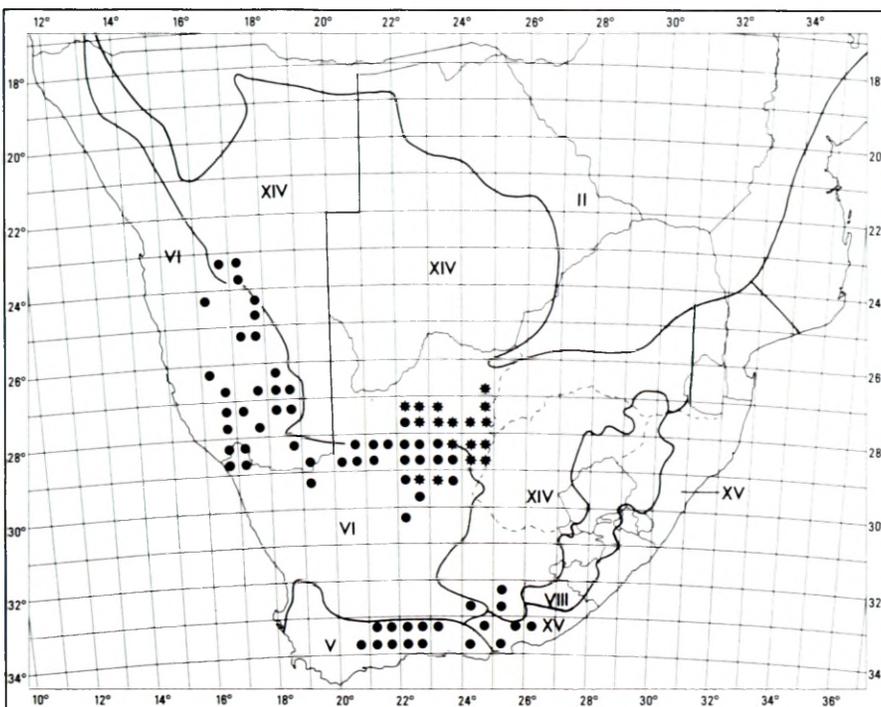


FIGURE 1. — Distribution of *Nymania capensis* in relation to the regional phytochoria of the Unesco/AETFAT/UNSO Vegetation Map of Africa (White 1983a). One symbol is shown for each quarter degree square. Circles represent herbarium specimens; stars, sight records (see text). II, Zambebian regional centre of endemism; V, Cape regional centre of endemism (enclaves of Karoo and Afromontane vegetation not shown); VI, Karoo-Namib regional centre of endemism; VIII, Afromontane archipelago-like regional centre of endemism; XIV, Kalahari-Highveld regional transition zone; XV, Tongaland-Pondoland regional mosaic.

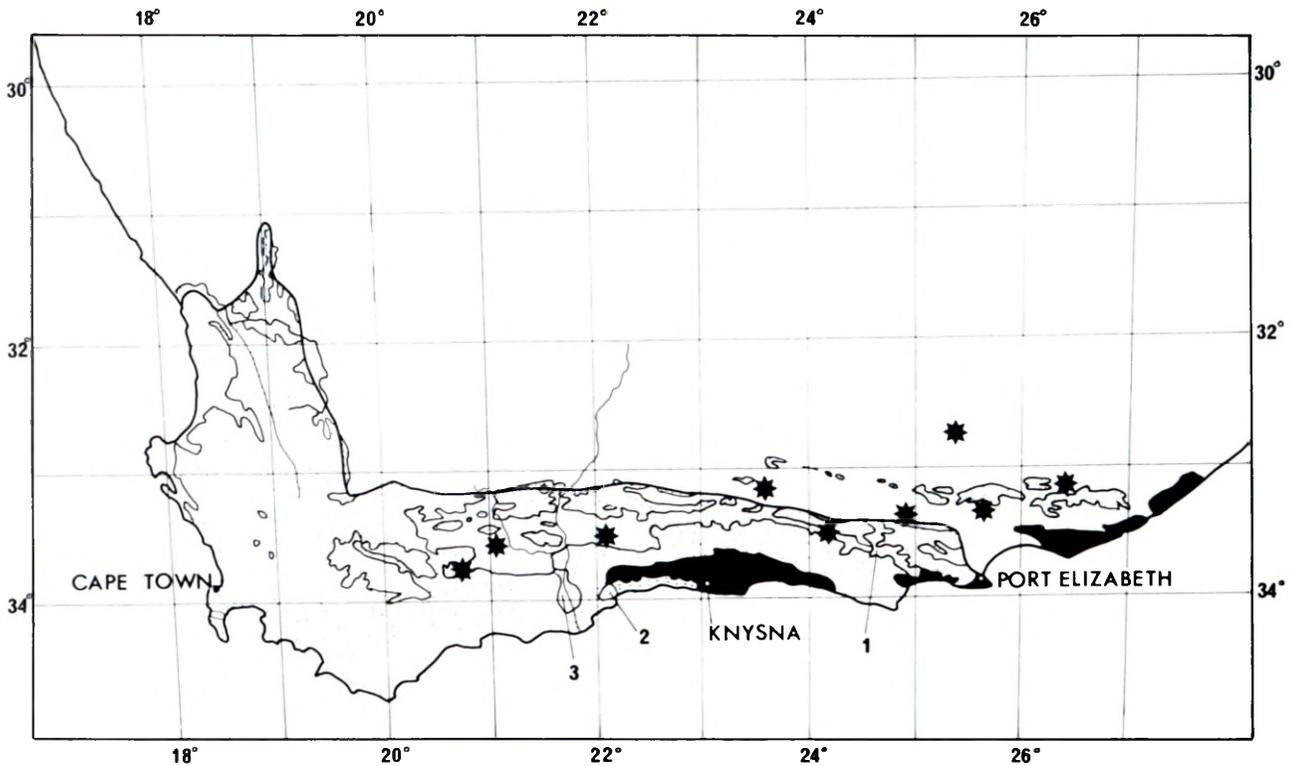


FIGURE 2. — Distribution of *Nymania capensis* in the southern part of its range in relation to the Cape Floristic Region as circumscribed by Goldblatt (1978) and Bond & Goldblatt (1984). Stipple represents fynbos and related types (Acocks's mapping units 43, 46, 47, 69, 70) which according to some workers (e.g. Taylor 1978; White 1983a) comprise the Cape Region *sensu stricto*. Black represents forest. Within Goldblatt's boundary, areas left white signify enclaves of Karoo vegetation (Acocks's mapping units 23, 25, 26, 31, 34), and valley bushland (Acocks's mapping unit 23) of Tongaland-Pondoland affinity. 1. Gamtoos River bushland; 2. Klein Brak River bushland; 3. Gouritz River bushland. Only selected localities (stars) of *Nymania capensis* are shown — sufficient to indicate its geographical range. I know of no records from characteristic Cape vegetation.

According to A. Gubb (*in litt.* 26 April and 28 May 1985) the fruits remain on the plant until the end of winter, i.e. August, which is the windy time of year. They are knocked off by the shaking of the shrub by wind action and by buffeting of the surrounding branchlets, whereupon they roll away across the ground with the wind. In the course of this movement the parchment-like capsule cracks open in many places and the seeds are released and presumably germinate with the spring rains in mid-October to late November. It is not known whether under exceptionally windy conditions the fruits or seeds ever become air-borne and are thereby transported for greater distances. The bright red capsules are conspicuous, but there is no evidence that this attracts potential dispersers.

#### Leaf fall

During the winter months the leaves become harder and begin to lose colour and by the end of winter up to 60% or more may have fallen. In spring new leaves appear and the remaining old leaves are shed. The plants are not truly evergreen since all the leaves are replaced each year and they are active for only about 9 months. Nor is the species truly deciduous since on all individuals at least some leaves are retained throughout the winter. Many other species in the northern Cape behave in a similar manner (A. Gubb *in litt.* 28 May 1985).

#### The occurrence of *Nymania capensis* in Ovamboland

This species is included in Rodin's posthumously published (1985: 113), fascinating and beautifully illustrated book on the ethnobotany of the Kwanyama Ovambos who live in the extreme north of SWA/Namibia. Rodin found one 10 m high tree with a gnarled trunk 1 m in diameter close to St Mary's Mission at Odibo. This is 650 km north of its nearest known locality. Rodin says that his plant has the same Kwanyama name (omunghudi) and the same use as *Boscia albitrunca* (Capparidaceae), and that this coincidence should be checked further. One of the specimens he cites (*Rodin 2665*, sterile, PRE), although atypical in some respects, is quite a good match for *B. albitrunca*, and the occurrence of *Nymania* in Ovamboland thus seems unlikely.

## 2. TURRAEA L.

### Sectio *Turraea*

Shrubs or trees. Flowers usually in sessile or pedunculate fascicles. *Bracteoles* inserted at base of the pedicels. *Calyx lobes* rarely foliaceous, united in lower half. *Style-head* distinctly wider than the style, capitate, with a single, terminal stigmatic surface, distinctly exerted beyond the anthers. *Capsule* usually more than 10 mm in diameter. *Seeds* usually more than 5 mm long; aril usually red or orange and

covering more than one-tenth of the surface of the seed.

1. *Turraea nilotica* Kotschy & Peyr., *Plantae Tinneanae*: 12, fig. 6 (1867).

*Distribution, ecology and relationships*

*T. nilotica* extends from the Sudan and Ethiopia southwards to the Transvaal. Since it occurs in six regional phytochoria it is a transgressor and can be referred to as an 'eastern wide'. It has corky, fire-resistant bark and frequently occurs in savanna woodland. It is closely related to *T. zambesica* (q.v.) and *T. robusta* Gürke which is found on the African mountains from Uganda and eastern Zaire to Malawi.

*Capsule structure and seed dispersal*

The fruit is a small, 10-valved, leathery capsule which becomes thinly woody after opening. Dehiscence is similar to that of *T. obtusifolia*. The seeds, however, which are 5 × 3 mm, have black testas and are superposed if both ovules in a locule develop to maturity. The small aril is said to be orange or reddish and in herbarium specimens appears to be almost completely concealed. The coloured illustration in Coates Palgrave (1956: 232) shows black seeds attached to a massive red central column; to judge from preserved material the size and nature of this column is not shown accurately. Field observations are needed. It seems that the septa remain membranous and that the small orange aril is largely confined to the adaxial surface of the seed except for a horn-like extension which protrudes beyond its apex. Nothing definite is known about dispersal. Rodgers (1976), who examined the rumen contents of 29 mature impala (*Aepyceros melampus*) from south-east Tanzania, found that fruits of *T. nilotica* were frequently present.

2. *Turraea zambesica* Sprague & Hutchinson ex Styles & F. White in *Boletim da Sociedade Brotariana*, sér. 2, 36: 71, fig. 1 (1962).

This species is only known from a small part of the Zambezi Region. It is confined to the Zambezi Valley and its tributaries. Its range lies partly within that of *T. nilotica* but at lower altitudes. It also extends further to the west. It would be interesting to compare these species in the field.

3. *Turraea obtusifolia* Hochstetter in *Flora* 27: 296 (1844).

*Distribution, ecology and relationships*

*T. obtusifolia* is widely distributed in southern Africa from Zimbabwe to the eastern Cape (Figure 3). It occurs throughout the greater part of the Tongaland-Pondoland floristic region (White 1983a) with a short penetration into the southern part of the Zambezi Region. It is a southern vicariad of the tropical species *T. mombassana* Hiern ex C. DC., which extends from Ethiopia to Malawi. The differences between them are given by White & Styles (1963).

*Variation and taxonomy*

The shape and size of the leaves are extremely variable. Variation in southern Africa is summarized in Figure 3, from which it can be seen that, although there are some geographical trends, the latter are insufficiently striking to serve the needs of formal taxonomy.

In general, plants with broad, rather deeply lobed leaves tend to be concentrated towards the middle of the range within about 200 km of Durban, the type locality, although the type specimen itself has relatively narrow, scarcely lobed leaves. In the past the name *T. obtusifolia* has been most frequently applied to the broad-leaved variants.

Towards the north and the south of the species range, variants with narrower, slightly lobed or unlobed leaves become frequent and locally predominate, though the broad-leaved variant occurs, at least sporadically, throughout the greater part of the area occupied by the species.

A narrow-leaved specimen from the extreme south was described by Casimir de Candolle (1878: 440) as *T. obtusifolia* var. *microphylla* and that name was subsequently applied to similar variants from the Transvaal (Burt Davy 1932), though Bremekamp (1933) gave the latter specific rank as *T. oblancifolia*. A detailed study of all the available, and by now copious, material has failed to reveal any discontinuities on which more than one taxon could be based.

To facilitate comparison, in Figure 3, variation in leaf shape has been assigned to two categories, namely (a) relatively narrow, unlobed or slightly lobed leaves and (b) broader, shallowly to deeply lobed leaves. Their distribution, based on all available material in the National Herbarium, Pretoria is as follows:

(1) Botswana and Transvaal: a, 67 specimens (93%); b, 5 specimens (7%).

(2) Swaziland and Natal south to Durban: a, 12 specimens (32%); b, 26 specimens (68%).

(3) Natal south of Durban, Transkei, eastern Cape: a, 24 specimens (70%); b, 10 specimens (30%).

Both variants also occur in the remainder of the species range outside southern Africa, namely in Zimbabwe and southern Mozambique. The leaves of *T. obtusifolia* are often variable on a single plant (Figure 3a) and their precise outline seems to depend, at least in part, on local conditions. Large, deeply lobed leaves occur most frequently inside the forest (e.g. *Ross & Moll 2309* from Hawaan).

Bremekamp suggested that *T. oblancifolia* also differs from *T. obtusifolia* in its depressed-globose not cylindrical style-head ('stigma') and in having longer, broader calyx-lobes which are not separated from each other by a wide sinus. As with leaf-shape, there seem to be broad geographical trends in these features but they are too imprecise to be taxonomically useful.

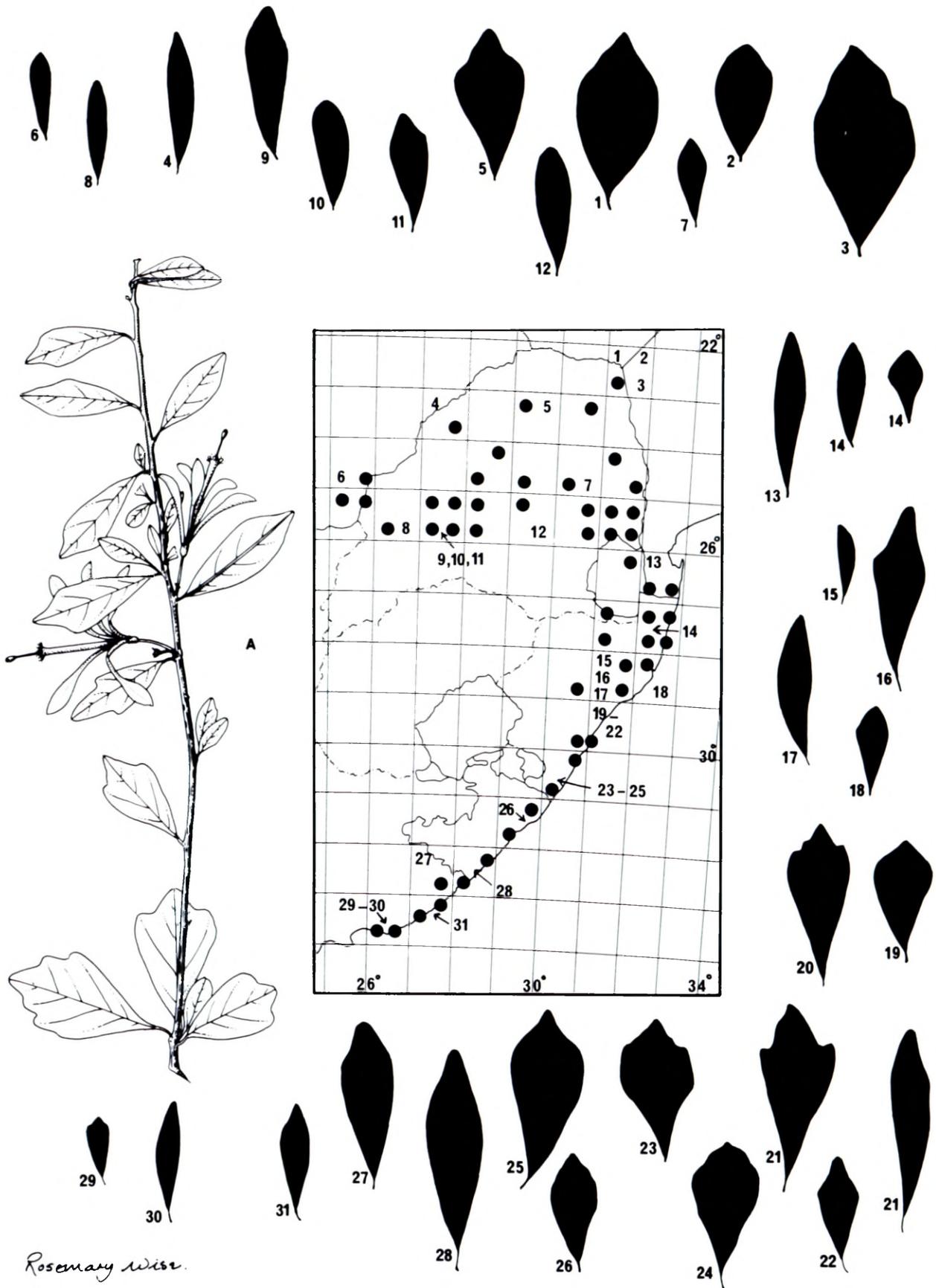


FIGURE 3. — *Turraea obtusifolia*. Pictorialized distribution map showing variation in southern Africa of shape and size of leaves. The specimens are numbered consecutively from north to south and the degree square from which each specimen was collected is indicated on the map. A. *Smith* 3636 from East London showing variation in leaf shape on a single twig; 1, *Van der Schijff* 3802; 2, *Ihlenfeldt* 2253; 3, *Van der Schijff & Marais* 3671; 4, *Fourie* 2627; 5, *Mogg* 24436; 6, *Hansen* 3296; 7, *Barnard* 387; 8, *Thode* A 1368; 9, *Codd* 722; 10, *De Winter* 8635; 11, *Van Vuuren* 451; 12, *Du Toit* 189; 13, *Pooley* 384; 14, *Reid* 496; 15, *Ward* 4387; 16, *Wells & Edwards* 77; 17, *Mthonti* 1; 18, *Ward* 1844; 19, *Moll* 3110; 20, *Ross & Moll* 2309; 21, *Wood* 5746; 22, *Krauss* 308 from Port Natal (Type of *T. obtusifolia*); 23, *Strey* 8065; 24, *Wylie* s.n.; 25, *Venter* 1035; 26, *De Winter* 8861; 27, *Comins* 1046; 28, *Pegler* 337; 29, *Tyson* s.n. (Kowie); 30, *Tyson* s.n. (Port Alfred); 31, *Jacot Guillarmod* s.n.

### Floral structure and pollination

The flowers are similar to those of *T. floribunda* but the proportions are slightly different. The petals are pure white and the style-head is cylindrical. The following observations were made in Zimbabwe (F. White, MS 1973). The flowers seem to last more than one night. By 10h30 they are no longer fragrant and some had withered. Some which were still fresh appeared to have been visited by moths the previous night, since the style had been pushed to one side and the pollen had been removed from the *receptaculum pollinis* on the side of the flower where the proboscis had entered the staminal tube. In some fresh but unvisited flowers, the style remained centrally placed and pollen occurred all the way round the *receptaculum pollinis*. In the open flower the anthers and appendages are disposed horizontally and it is unlikely that they would come into contact with the proboscis of a visiting hawk moth.

### Capsule structure and seed dispersal

The fruit is a small, 5-valved, leathery loculicidal capsule which becomes woody after dehiscence. The rather thin valves and outer parts of the septa separate from the inner parts of the septa and the central placental axis, to which the 6–10 seeds remain firmly attached. The seeds, which are 5.5 mm long and have a bright red, shining testa, are tightly packed together, and are very conspicuous against the pale straw-coloured inner surface of the now horizontal or reflexed lobes of the capsule.

The white aril is very small and is completely hidden unless the seed is removed. It consists of two thin fleshy wings which are free except for a narrow attachment along the raphe. It covers less than one sixth of the surface of the seed and scarcely extends beyond the margins of the adaxial cavity.

The seeds of *T. obtusifolia* appear to mimic the more conspicuously arillate seeds of other plants, and it is possible that fruit-eating birds are deceived by their appearance and play some part in their dispersal without obtaining much nourishment from them. It is also possible that ants eat the arils of fallen seeds and play a local role in dispersal, as they are said to do (Milewski & Bond 1982) in the case of some other South African plants with small arils (e.g. *Pterocelastrus*).

Attractive and informative coloured photographs of the fruits of *T. obtusifolia* have been published by Onderstall (1984, opp. p. 122 and a newspaper cutting in PRE).

4. ***Turraea floribunda*** Hochstetter in Flora 27: 297 (1844).

### Distribution and ecology

*T. floribunda* is an 'eastern wide' which extends in various types of forest from the Sudan and eastern Zaire to southern Africa. In tropical Africa its distribution is mostly scattered.

### Floral structure and pollination

The flowers open at night and are visited by hawk moths which arrive *en masse* at the trees at dusk.

They stay for 15–30 minutes and then leave together (T.K. Lowrey *in litt.* 21 June 1985). Further information is not available. It would seem that the elongate, divergent, greenish white petals act as a distant visual attractant and that the much smaller radiating staminal appendages enable the pollinator to focus more precisely on the extremely narrow entrance to the staminal tube. The anthers dehisce before the flower opens and pollen grains may be seen adhering to the emerging discoid style-head which appears to function as a *receptaculum pollinis* (F. White, pers. obs.). At this stage the apical stigmatic surface, which is less than half the diameter of the style-head, is free from pollen grains. In the mature flower the style-head is far-exserted and in some flowers the style is bent through nearly 90 degrees near its apex, and possibly thereby places the stigma in a suitable position for the reception of pollen. The stigma is minute, especially in relation to the size of the flower and its pollinators. It would be interesting to know precisely how pollen transfer is brought about.

Style length varies in different parts of the geographical range of *T. floribunda*. In southern Africa it is usually less than 40 mm long whereas in east Africa it can reach 100 mm. It would be worth investigating the significance of this in relation to its pollinators.

### Capsule structure and seed dispersal

The fruit is a 10-valved leathery capsule with very thick (4–6 mm) valves which, after dehiscence, become woody and divergent like the rays of a starfish; ultimately they are sometimes reflexed. Dehiscence is similar to *T. obtusifolia* but relatively few seeds mature, normally only 5–6 out of a possible 20. The seeds have an orange testa which contrasts with the whitish fleshy aril. The latter covers approximately one third of the seed, and its margins are visible flanking the seed. The seeds, which are sometimes superposed, are small in relation to the size of the capsule and are individually rather than collectively conspicuous. Nothing is known about their dispersal.

Sectio **Nurmonia** (Harms) F. White, comb. et stat. nov.

*Nurmonia* Harms in Berichte der Deutschen botanischen Gesellschaft 35: 74–82 (1917a). Type species: *Turraea pulchella* (Harms) Pennington in Pennington & Styles (1975).

Suffrutices. Flowers solitary or in 2–3-flowered cymes. Bracteoles inserted on the pedicels. Calyx lobes foliaceous, free almost to the base. Style-head only slightly wider than the style, with 5 stigmatic lobes at apex, not or only slightly exserted. Capsule up to 8 mm in diameter. Seeds c. 3 mm long; aril whitish and inconspicuous, covering about one tenth of the surface of the seed.

5. ***Turraea pulchella*** (Harms) Pennington in Blumea 22: 454, fig. 3d (1975). Type: Transkei: near Kentani, rare, 330 m, fl. March 1903. Pegler 730 (B. holo. †?). Several other specimens with the same number were also collected by Pegler near Kentani, but on different dates between April 1900 and Oc-

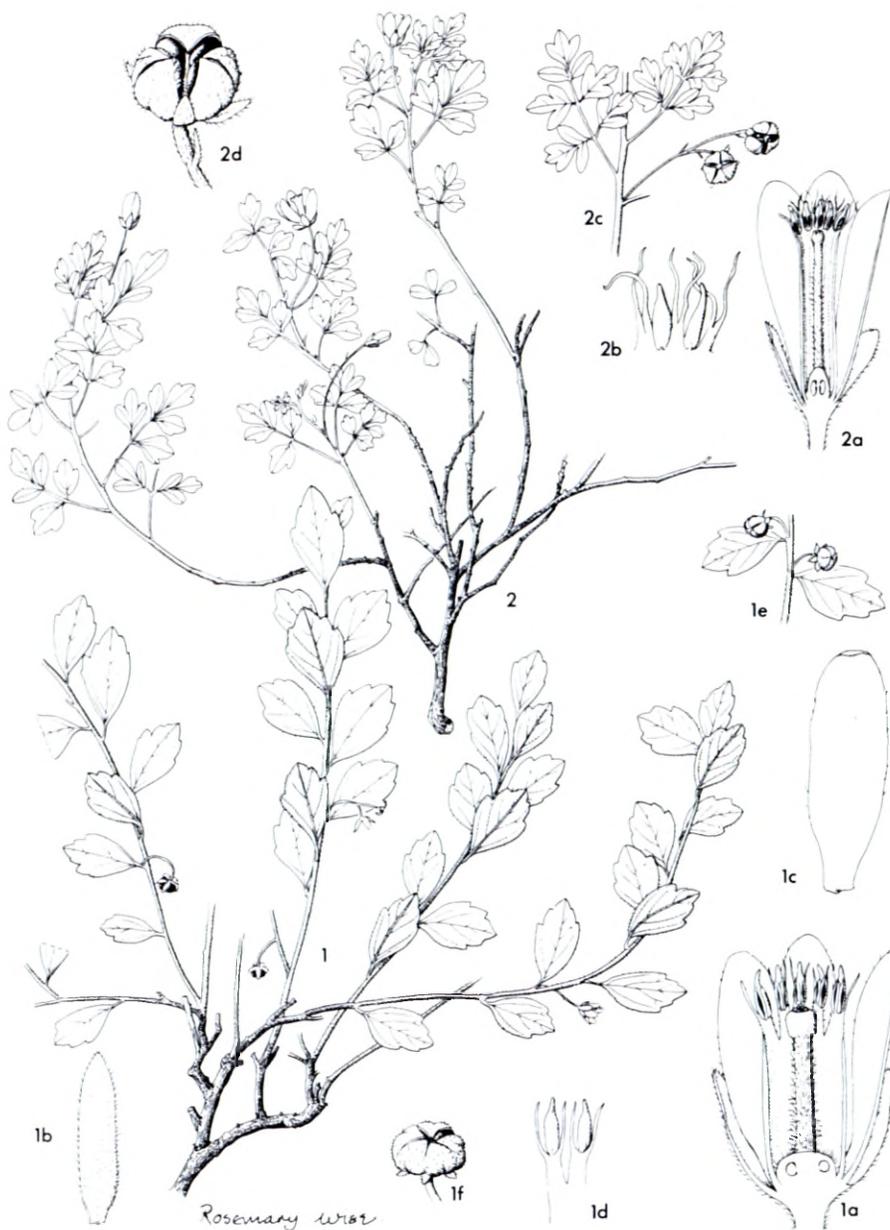


FIGURE 4. — 1. *Turraea pulchella*, habit  $\times 0.4$ ; 1a, flower in longitudinal section,  $\times 5.7$ ; 1b, sepal,  $\times 5.7$ ; 1c, petal,  $\times 5.7$ ; 1d, part of staminal tube and anthers,  $\times 5.7$ ; 1e, fruit and leaves,  $\times 0.4$ ; 1f, fruit  $\times 1.4$  (all from Pegler 730). 2. *Turraea streyi*, habit,  $\times 0.4$ ; 2a, flower, in longitudinal section,  $\times 2.8$ ; 2b, anthers and appendages,  $\times 5.7$ ; 2c, fruiting branchlet,  $\times 0.4$ ; 2d, fruit,  $\times 1.4$ ; (all from Srey 6878).

tober 1913; among them the following is selected as neotype: Transkei, Kentani District, 305 m occasional, valley, bank of stream, rare, fl., frt. March 1903, Pegler 730 (K, neo!., here designated, BOL!). The neotype may be a duplicate of the holotype but the matter is by no means certain.

*Nurmonia pulchella* Harms: 80, fig. 1 (1917).  
*Turraea heterophylla* sensu Pegler: 12 (1918).

#### Distribution, typification and ecology

Only known from Kentani District in Transkei where it was collected by Miss Alice Pegler several times between Apr. 1900 and Oct. 1913. Miss Pegler gave the same number to all her gatherings which were distributed to several herbaria. In addition to the neotype I have seen the following:

TRANSKEI. — 3228 (Kentani Distr.): valleys 610 m, fl.-buds Apr. 1900, Pegler 730 (PRE!); occasional, fl. Mar. 1902, Pegler 730 (SAM!); 305 m, fl., frt. Apr. 1903, Pegler 730 (SAM!); 305 m, occasional, fl., frt. 15 Oct. 1904, Pegler 730 (PRE!, SAM!); 305 m, hill slopes, occasional, fl., frt. 10 November 1905, Pegler 730 (FHO!); 365 m, along valleys, fl. Oct. 1911, Pegler 730 (PRE!);

365 m, thick, woody underground stem, fl., imm. frt. 15 Oct. 1913, Pegler 730 (PRE!); 365 m, about 6–10 in. above ground, fl. Oct., Pegler 730 (K!) No information given: frt., Pegler s.n. (PRE ex Herb. Marloth!); fl., frt., Pegler 730 (P!).

*T. pulchella*, it seems, has a very restricted distribution and has not been collected for more than 70 years. Miss Pegler did not give precise details on her labels, but according to Gunn & Codd (1981) most of her specimens were collected from within 13 km of Kentani Village. They appear to have come from various localities between 305 and 610 m. The only ecological information she provided (Pegler 1918) is that it grows among tall grass. Herbarium specimens suggest that *T. pulchella* can tolerate, and may possibly be adapted to, at least light, fires. On the herbarium specimens all the shoots that bear leaves belong to the current year's growth. They arise from short, branched, older, woody stems, some of which look as if they might have been burnt back in previous years (Figure 4.1). In its manner of growth *T. pulchella* resembles the geoxylic suffrutices described from tropical Africa by White (1976).

According to Pegler (1918) fires in Kentani District had greatly increased during her life-time and had led to an impoverishment of the flora. This species must surely qualify for inclusion in future editions of 'Threatened plants of southern Africa' (Hall *et al.* 1980).

#### *Floral structure and pollination*

Interpretation of herbarium specimens is difficult but it is possible that there is a primitive *receptaculum pollinis* mechanism. In one flower which was dissected an anther was found to be firmly attached to the style-head.

#### *Capsule dehiscence and seed dispersal*

The small capsules and seeds are likely to be inconspicuous to birds, especially as the plant is said to grow among tall grass. In herbarium specimens, in capsules beginning to dehisce, the seeds readily become detached from the placenta. In the field, when they fall to the ground, it is possible that they are dispersed by ants. Occasional dispersal by small seed-eating birds cannot be ruled out. The extremely restricted distribution of *T. pulchella* suggests that dispersal, whatever the means, is not very efficient.

#### 6. *Turraea streyi* F. White & B.T. Styles, sp. nov.

Species nova inter species Africanas solum prope *T. pulchellam* (Harms) Pennington ob habitum suffruticosum, lobos calycis foliaceos, stylum brevem, semina minuta et capsulam quinquevalvem ponenda; ab omnibus speciebus generis foliis compositis differt.

TYPE. — Natal, 3030 (Port Shepstone): St Michael's-on-Sea, Deppe's Farm (–CD), a heavily browsed 'bush' in bushveld, white flowers, fl. 19 Sept. 1966, *Strey 6876* (PRE, Sheet 1 holo.!: NH!, NU, 2 sheets!).

Among African species only to be placed close to *T. pulchella* (Harms) Pennington on account of its suffruticose habit, foliaceous calyx-lobes, short style, minute seeds and 5-valved capsule; differs from all species in the genus in its compound leaves.

Suffrutex up to 0.75 m high; branchlets, inflorescence-axes and both leaf surfaces sparsely to densely setulose. *Leaves* up to 70 mm long, very variable, trifoliolate, twice-trifoliolate or imparipinnate with 3–5 deeply lobed or trifoliolate divisions; lobes rounded to acute. *Flowers* axillary, solitary or in lax 2–3-flowered cymes; pedicel or peduncle slender, up to 35 mm long, bracteoles minute, filiform,  $\pm 1$  mm long. *Calyx* 3–5 mm long, hispidulous, lobes foliaceous, oblong-elliptic, acute, free almost to the base. *Petals* white, glabrous, 8–11  $\times$  3–4 mm, broadly spatulate. *Staminal tube* 7–9 mm long, hairy in upper half inside, not split at apex; appendages paired, filiform, alternating with and much longer than the anthers; anthers long-apiculate, dehiscent by very short slits in lower half. *Ovary* densely hairy, 5-locular with 2 collateral ovules per locule; style 7–10 mm long, included or very slightly exerted, hairy in lower half; style-head capitate, less than 1 mm in diameter with a terminal, 5-lobed,

coroniform stigma. *Capsule* 5  $\times$  8 mm, up to 10-seeded, otherwise as in *T. pulchella*. *Chromosome number*:  $2n = 36$  (*Strey 9288* South Africa). Figure 4.2.

*T. streyi* is named in honour of its discoverer, Rudolf Georg Strey, distinguished contributor to South African botany who guided the senior author of this species through parts of Natal, the Transkei and the eastern Cape in 1973.

NATAL. — 2931 (Stanger): King Hamlyn's Farm (–AD), scrub forest, small sub-woody plant in the lower storey, 0.25 m, fl. 19 Sept. 1971, *Moll 5502* (PRE), 3030 (Port Shepstone): Deppe's Farm (–CD), next to 'Skyline', St Michael's-on-Sea, erect 'herb' in heavily grazed grassland, up to 0.4 m high where protected; flowers white; locally fairly common, fl., frt. 10 December 1968, *Ross 1853* (FHO!, NH!, PRE!); Uvongo road, bush margins; fl., frt. 27 Nov. 1969, *Strey 9288* (NH, 3 sheets!).

#### *Distribution and ecology*

*T. streyi* is only known from two widely separated localities in the Tongaland-Pondoland phytogeographical region of the Unesco/AETFAT/UNSO 'Vegetation map of Africa' (White 1983a).

It occurs both inside and at the edges of scrub forest and bushland, and in both rank and heavily grazed grassland. At the type locality (White, MS 1973) the vegetation is a mosaic of grassland and open bushland in which *Strelitzia nicolai* Regel & Koern., *Dalbergia obovata* E. Mey., *Chaetacme aristata* Planch., *Acacia karroo* Hayne, *Psidium guajava* L., *Rhus chirindensis* Bak. f., *Ekebergia pterophylla* (C. DC.) Hofmeyer, *Loxostylis alata* Spreng. f. ex Reichb. and *Zanthoxylum capense* (Thunb.) Harv. are conspicuous.

Its growth form varies according to local ecological conditions. In the shady undergrowth of forest (*Moll 5502*) the stems are slender and the leaves 3-foliolate and shallowly lobed. In rank grassland the stems are elongate and only sparsely branched. When it is heavily browsed (*Strey 6876*) it is richly branched and shrubby at the base. Nothing is known about its response to fire, but some specimens (e.g. *Strey 6288*) look as if the previous year's growth had been singed and killed back by fire. In its habit, *T. streyi* is similar to a composite, *Schistostephium hepatalobum* (DC.) Oliv. & Hiern, which grows with it, and mixed gatherings have been made. Sheet 2 of *Ross 1853* (FHO) is *Schistostephium*.

#### *Floral structure and pollination*

The flowers are similar in structure to those of more typical species of *Turraea* except for their smaller size, proportionally broader petals and much less well-differentiated style-head. They possibly have a primitive type of *receptaculum pollinis* mechanism. In one unopened flower on a herbarium specimen the anthers had already dehisced and some grains were adhering to the style-head, though none were found on the stigmatic crests. The anther-slits are about the same length as the style-head but they produce many more grains than can be accommodated on its surface. Most of the grains were entangled among the hairs between and just beneath the anthers.

### *Capsule dehiscence and seed dispersal*

The capsules are remarkably similar to those of *T. pulchella* and the seeds are possibly dispersed in a similar way.

### 3. MELIA L.

A small genus of three species. Two are indigenous to Africa. *M. bombolo* Welw. occurs in rain forest in Gabon, Congo, Zaire and Angola, whereas *M. volkensii* Gürke is a conspicuous emergent tree in deciduous bushland in parts of the Somalia-Masai Region in east Africa. The third species, *M. azedarach* L., as a wild plant occurs in the more seasonal forests of the Far East from India to Australia (Mabberley 1984). It has been widely planted for timber and especially for ornament throughout the tropics and subtropics, including all the warmer parts of southern Africa.

#### *Melia azedarach* L.

Two groups of variants of this species have been widely planted in Africa: (a) The 'Wild' plant or White Cedar is often grown for forestry purposes, but no herbarium specimens have been seen from southern Africa; (b) What Mabberley refers to as the 'Indian Cultivars', which are widely known as Persian Lilac and less often as Bead-tree.

In southern Africa, and to a lesser extent elsewhere, the nomenclature of this plant, both popular and scientific is confused. Linnaeus described two species of *Melia* with very similar names, namely *Melia azedarach* and *M. azadirachta*. The latter, the Neem or Nim Tree, is now placed in a different genus and is known as *Azadirachta indica*. Because of the similarity of their names, the one is often mistaken for the other. For this reason, much of the information on medicinal and other uses given under *Melia azedarach* by Watt & Breyer-Brandwijk (1962) and by some other authors refers to *Azadirachta*. Linnaeus's two species are also stated to be synonymous in a recent publication on South African introduced trees (Von Breitenbach 1984). In the latter work the name 'Syringa' is proposed as the National Name for *Melia azedarach*. This is unfortunate since *Syringa* is a well-known generic name in Oleaceae and has also been used as a popular name for species and cultivars of *Philadelphus* (Saxifragaceae sensu Engler).

The following notes refer to typical Persian Lilac. In addition, the cultivar 'Umbraculifera', the Texas Umbrella Tree, a mutant form with a flattened crown, is sometimes planted in gardens.

#### *Distribution and ecology in southern Africa*

*M. azedarach* has been planted in all the warmer parts of southern Africa. It is widely naturalized and locally has become a pest. As early as 1906 it was established near Barberton (Burt Davy 1932). In the Kruger National Park it is liable to supplant the natural vegetation in the river valleys and is difficult and expensive to eradicate (Van Wyk 1984). It is also invasive in Natal (W. R. Bainbridge pers. comm.). According to Henderson & Musil (1984)

*Melia azedarach* is the most widespread and aggressive of the invasive introduced trees in the Transvaal. It is highly penetrative and is often found far from buildings. It is drought- and frost-resistant and has become a roadside weed and has invaded water-courses and natural, but presumably disturbed, vegetation including bushland and forest. Henderson & Musil suggest that the few remaining relict stands of forest in the Transvaal are liable to be replaced by exotics such as *Melia azedarach*, though this may be somewhat exaggerated. They did not apparently study dispersal of this species.

#### *Fruit structure, toxicity, chemistry and dispersal*

The fruit is a drupe. Until recently the most thorough investigation of its properties was by Steyn & Rindl (1929), who refer to the conflicting evidence of earlier work. Some of the publications they cite state that children can eat the fruit without inconvenience whereas others mention fatal cases of poisoning. Steyn & Rindl found that none of their experimental animals would ingest the drupes which to man have an unpleasant smell and an intensely bitter, nauseating taste. It was necessary to force feed them with extracts of ground-up fruits by means of a stomach tube. Pigs, sheep, goats, rabbits and guinea-pigs were found to be affected by *Melia* poison, with pigs the most susceptible. For pigs the lethal dose, however, was quite large, 150–200 grams of drupes for an animal weighing 75 kilograms. By contrast, Muscovy ducks were not killed even by relatively high doses. It was pointed out that different kinds of wild birds are fond of the fruit but ingest only the flesh and discard the kernels, and that the locus of the toxins, flesh, kernel or both, was not known at that time. Watt & Breyer-Brandwijk devote several pages of uncritical and inconclusive discussion to the toxicity or otherwise of the *Melia* fruit, from which it is difficult to draw any conclusions.

Oelrichs *et al.* (1983) have recently extracted and identified four meliatoxins (a group of limonoids) from the flesh of *Melia azedarach* and confirmed its highly toxic nature. Their experimental pigs showed rapid muscular contractions within 2–4 hours of drenching, followed by collapse, rapid heart beat and dilated pupils. Death occurred after about 30 hours. The meliatoxins are believed to have been responsible for the acute nervous symptoms and rapid death in pigs, though other compounds in the fruit are thought to have other adverse effects. Oelrichs *et al.* obtained their material from five localities in Queensland, where the tree is native. The concentration of meliatoxins in the fruit was variable and in three cases they were absent. The extent to which this variability may depend on the degree of ripeness of the fruit is not clear and requires further investigation. One of the meliatoxins extracted from *Melia azedarach* is very similar structurally to an insect antifeedant, trichilin A, which occurs in *Trichilia emetica* ('roka'; Nakatani *et al.* 1981). The limonoids in the flesh of the fruit are different from those of the seed (D. A. H. Taylor pers. comm.).

Recent work has shown that *M. azedarach* is very variable chemically. It almost seems that no trees are alike, though the overall pattern is constant enough.

Kraus *et al.* (in press in *Tetrahedron*; preprint sent to D. A. H. Taylor, pers. comm.) have recently discovered a set of limonoids in cultivated plants of *M. azedarach* from Greece which are different from those that Oelrichs found. They have also confirmed that azadirachtin occurs in both *Melia* and *Azadirachta*.

Only casual observations are available on the dispersal of *Melia azedarach*. In Australia, where it is native, its fruits are eaten by the Topknot pigeon (*Lopholaimus antarcticus*) in August and September, when its preferred fruits (species of Lauraceae and Palmae) are scarce (Frith 1957). They are not an important item in the diet of this species, although they are said to form the principal winter food of the Wompoo Pigeon (*Ptilinopus magnificus*). For southern Africa, Rowan (1967) records that the fruits are eaten by species of Mousebird (*Colius*) and the Grey Loerie (*Corythaioxoides concolor*). If eaten too freely they narcotize the Loerie which has been seen to fall from the tree in which it was feeding. A similar reaction has not been seen to occur in the Mousebird. In Natal, according to W. R. Bainbridge (pers. comm.) *M. azedarach* is dispersed by fruit bats. In Durban and Pietermaritzburg it is now unpopular as a garden plant because the bats often leave unsightly excrement stains on the walls of buildings.

The dispersal biology of *M. azedarach*, both in its native lands and elsewhere, it seems, is complex. The principal function of the meliatoxins is probably to protect the developing fruit from predators. It would be interesting to know the extent to which they are present in the fully ripe fruit and, if so, the influence this has on dispersal.

#### 4. AZADIRACHTA *Adr. Juss.*

*Azadirachta indica* *Adr. Juss.* \*in Mémoires de Muséum nationale d'histoire naturelle 19: 221 (1830).

The Neem Tree is a native of India and Burma. It is widely planted in the drier parts of Africa for timber and ornament, but is not often seen in southern Africa. For semi-arid regions, Radwanski & Wickens (1981) advocate the use of *Azadirachta indica* in an alternative approach to agricultural production which relies on vegetative fallow for the recycling of plant nutrients and is closely linked with rural industry based on plant products. The whole plant is medicinal. One of the most powerful naturally occurring insect antifeedants, the limonoid azadirachtin, occurs in this species. It can be used to control various types of insect larvae including locusts. At concentrations as low as a few parts per million it is active against larvae of Lepidoptera (Zanno *et al.* 1975). Azadirachtin acts by appetite suppression and eventually the larvae die of starvation. It also inhibits ecdysis and so kills insects. It is especially active against the tobacco budworm, which is a serious pest, and is being used in field test (D. A. H. Taylor pers. comm.). Its molecule is too complicated for economic synthesis, but the use of crude extracts of

limonoids from the Neem Tree and other Meliaceae including *Melia azedarach* is being investigated (Pickett 1985). The fruit pulp of *Azadirachta* apparently has not yet been analysed (D. A. H. Taylor pers. comm.) and it is not known whether it is toxic. In Ghana the fruits are extensively distributed by fruit bats (Ayensu 1974). Viable seeds have also been obtained from the dung of baboons (Lieberman *et al.* 1979).

#### 5. EKEBERGIA *Sparrrm.*

1. *Ekebergia capensis* *Sparrrm.* in Svenska vetenskapsakademiens handlingar 40: 282, fig. 9 (1779); White & Styles: 316, fig. 62 (1963) Styles: 409 (1974); Styles & White. Meliaceae in Flora of Ethiopia (in press).

*E. senegalensis* *Adr. Juss.*: 234, 273 (1830); Exell & Mendonça: 316 (1951); Keay: 705 (1958); Staner & Gilbert: 208 (1958); Styles: 410 (1974), *synon. nov.*

*E. mildbraedii* *Harms*: 229 (1917b); Staner & Gilbert: 210, fig. 23 (1958), *synon. nov.*

#### *Distribution, ecology and taxonomy*

*E. capensis* is widespread on the African mainland extending from Senegal eastwards to Ethiopia and from there southwards, mostly in montane and riparian forest, to the forests of the southern Cape. There is also a westward extension into Shaba, Zambia, Zimbabwe and Botswana and outlying populations occur in Angola. It is absent from most of the lowland rain forests of the Guineo-Congolian Region, but occurs locally towards their northern fringes and extremely rarely in their interior as at Yangambi in the heart of the Zaire basin. Throughout most of its range *E. capensis* is a forest species, but in places, from west Africa to Uganda, it can be found in savanna woodland. Because it occurs in more than one major vegetation type and more than one regional phytochorion, it is an ecological and chorological transgressor (White 1978a: 475; 1978b). In common with many other widespread species, *E. capensis* is very variable morphologically. The pattern, however, is poorly correlated with ecology and geography and it would be difficult to justify the recognition of more than one taxon.

#### *Variation in southern Africa*

Variation in leaflet shape and size (and some other features) in southern Africa is summarized in Figure 5. In leaflet shape, most specimens from southern Africa closely resemble *E. capensis* from the mountains of east Africa as far north as Ethiopia, though some have smaller or relatively narrower leaflets. A few specimens, e.g. *Renny 121* from Letaba, Transvaal, have a densely tomentose lower leaflet surface. Similar variants occur sporadically elsewhere, and in Malawi were formerly given specific rank as *E. buchananii* *Harms* (see White & Styles 1963.)

In southern Africa the most distinctive variant occurs towards the southern extremity of the range of the species in the Transkei and Cape Province south-eastwards from Kentani. These plants, e.g. *Albany Museum No. 25979*, are characterized by slow-grow-

\* The precise date of publication is uncertain (see Stafleu & Cowan, *Taxonomic literature*, edn 2, vol. 2: 476, 1979).

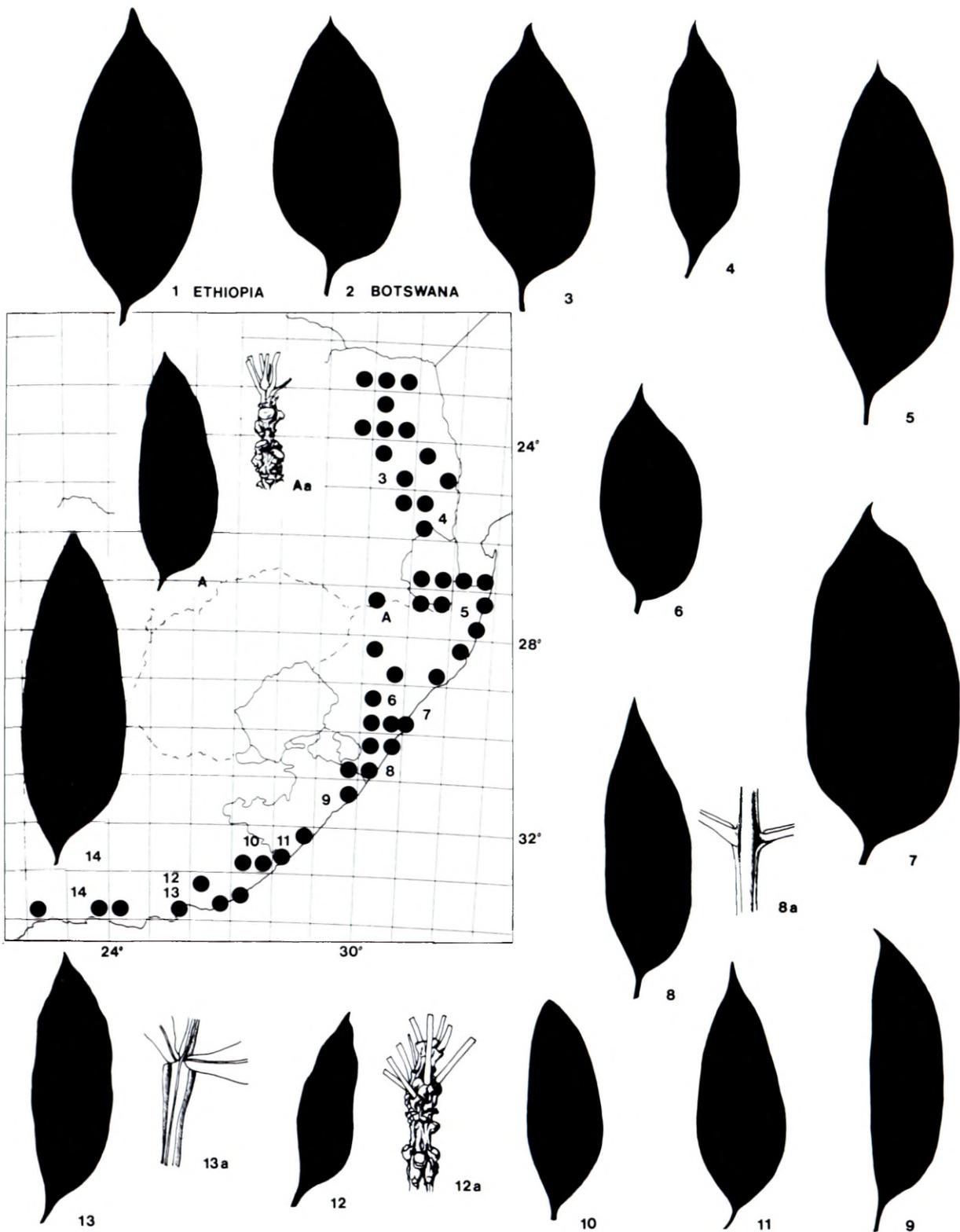


FIGURE 5. — *Ekebergia capensis*. Pictorialized distribution map showing variation in southern Africa of: leaflet-shape and -size, leaf-rhachis, and leaf-scars on branchlets. Specimens are numbered consecutively from north to south. For leaflets No. 3–14, the number is also shown on the map inside the degree square from which the specimen it came from was collected. 1, *Bos* 9720; 2, *Smith* 1471 from Dikgathong, SE 1922; 3, *Van Greuning* 502; 4, *De Souza* 81; 5, *Moll* 4927; 6, *Moll* 1724; 7, *Ward* 5848; 8, *White* 10527; 9, *Strey* 10123; 10, *Flanagan* 818; 11, *Pegler* 849; 12, and 12a, *Transvaal Museum*; 13, and 13a *Olivier* 1101; 14, *Marloth* 7433. Leaflets and branchlets,  $\times 0.6$ ; leaf-rhachis,  $\times 2.4$ . A, *Devenish* 1039 from N Natal showing remarkable similarity to the Cape variants. Drawn by Gillian Condy.

ing shoots with very prominent leaf scars (Figure 5.12a), short leaves with small closely spaced leaflets and a distinctly winged rachis (Figure 5.13a), and short inflorescences. Both the Cape and the northern variants are sometimes grown for ornament, as in Pretoria, and those who have been able to compare them as living plants sometimes express surprise that they should be regarded as conspecific. As Figure 5 clearly shows, the overall pattern is too diffuse to permit taxonomic subdivision. The populations between Port Shepstone and Kentani are intermediate, and some populations south of Kentani, especially those in the more luxuriant forests of Alexandria and Knysna (e.g. *Marloth 7433*), more closely resemble the northern plant. Furthermore, specimens collected at high altitudes from several localities in the north resemble the Cape variants in some features. They include: *Devenish 1039* from Donkerhoek, Natal (Figure 5.A.Aa); *Torre & Paiva 12731* from Serra Zaira, Mozambique and *Paulo 1004* from Murua Nysigar Peak, Kenya.

2. ***Ekebergia pterophylla* (C. DC.) Hofmeyr** in *Journal of Botany, British and Foreign* 63: 57 (1925).

*Trichilia pterophylla* C. DC.: 581 (1894).

*Trichilia alata* N. E. Br.: 160 (1896). In the protologue the following types are cited: Natal, Umhloti, *Wood 1022* (K!) and Groenberg, *Wood 1043* (BOL!, K!, PRE!, SAM!) and near Pine-town, *Wood 3403* (K!), *5439* (K!); Transvaal, near Barberton, *Galpin 1226* (BOL!, K!) and at Upper Moodies, *Galpin 1083* (BOL!, K!, PRE!, SAM!). Of these, the Kew specimen of *Wood 1043* has been labelled as the 'type' by N. E. Brown and is here designated as a lectotype.

#### *Distribution and ecology*

*E. pterophylla* is a Tongaland-Pondoland near-endemic species. It is almost confined to the Tongaland-Pondoland regional mosaic but also intrudes a short way into the south-eastern extremity of the Zambezi Region (White 1983a & b). It occurs in evergreen and semi-evergreen bushland and scrub forest, especially in rocky places. Towards the northern end of its range, as at Blyde Canyon Nature Reserve (Transvaal, 2430), its associates include typical Zambezi species such as *Combretum apiculatum* Sond., *C. molle* R. Br. ex G. Don, *C. zeyheri* Sond., *Lannea discolor* (Sond.) Engl. and *Pterocarpus angolensis* DC. Near its southern limit, as at the Umzimkulu Gorge (Natal, 3030) and other localities nearby, the Zambezi element is almost totally lacking and Tongaland-Pondoland endemic species, such as *Anastrabe integerrima* E. Mey. ex Benth., *Burchellia bubalina* (L.f.) Sims, *Diospyros simii* (Kuntze) De Winter, *Loxostylis alata* Spreng. f. ex Reichtb., *Protorhus longifolia* (Bernh.) Engl. and *Rhynchocalyx lawsonioides* Oliv. occur with it (White, MS 1973).

## 6. TRICHILIA P. Br.

### *The correct name for Trichilia emetica Vahl*

The earliest published binomial for this plant appears to be *Elcaja roka* Forskål\*. It is included in a list of useful plants entitled *Plantarum distributio practica* as a *nomen nudum* on page xcv of Fors-

kål's *Flora Aegyptiaco-arabica* (1775). This work was published posthumously by Carsten Niebuhr, a mathematician and astronomer, who was the only survivor of the ill-fated Danish Expedition to Arabia Felix on which Forskål died (Hansen 1964). Niebuhr was not very well qualified to edit Forskål's work, which after publication was criticized by some botanists for its inaccuracies. Although the generic name *Elcaja* was validly published, the binomial *E. roka* was not.

Fifteen years after the publication of Forskål's flora, the Danish botanist Martin Vahl (1790) attempted to make good its deficiencies. He realized that *E. roka* is a *Trichilia*, and described it as *T. emetica*, citing *Elcaja* in synonymy. Vahl's name was used by all botanists until 1923 when Chiovenda transferred *E. roka* to *Trichilia* in the mistaken belief that it had been validly published, a view which was endorsed by Brenan (1953). The name *T. roka* was adopted in most floras during the next 10 years (e.g. Keay 1958; Staner & Gilbert 1958; White 1962). It was also used in South Africa in some non-botanical works dealing with poisonous plants (Watt & Breyer-Brandwijk 1962) and garden trees and shrubs (Van der Spuy 1971), and still persists sporadically in the phytochemical literature (Nakatani *et al.* 1981).

After consulting the late J. E. Dandy, a leading authority on nomenclature, White & Styles (1963) reverted to the use of *T. emetica*, but did not publish

\* This is the spelling which appears on the title page of Forskål's book. It has been very widely used, either in full or in an abbreviated form, in taxonomic literature, including the *Index Kewensis*, for more than 200 years. This spelling was also adopted by Vahl, who wrote a comprehensive but insufficiently appreciated commentary on Forskål's work.

In a scholarly paper Friis & Thulin (1984) have argued that the correct spelling is *Forskål*, and this variant has appeared with or without the diacritical sign in some recent literature including an index of recommended author abbreviations (Meikle 1980).

Those who advocate such changes, it seems to me, are missing the point. Forskål and his relatives at different times spelt their name in different ways (Shakespeare was equally inconsistent), which suggests that the precise spelling of their names was of little importance to them. The citation '*Elcaja roka* Forskål' is not intended to be a statement about the correct spelling of its author's name but is merely a device to distinguish Forskål's plant from any others which may independently have been given the same name.

Recent editions of the *International code of botanical nomenclature* have encouraged instability of plant names in a misguided quest for equity and scholarship. It is true that the current edition permits the proposal of *nomina specifica conservanda*, but this may be too little and too late. Without a change of heart among those who enjoy upsetting established nomenclature this opportunity may be largely ineffective. The altering of conventional spellings of author's names has the same unfortunate consequences as changing the names of plants. It can only serve to confuse the non-specialist. It is recommended that for botanical purposes the spelling of Forskål's name as given in the *Flora Aegyptiaco-Arabica* should be conserved, and that the formation of all Latin scientific names based on it (past and future) should be standardized. The Code as it stands, however, does not permit this and needs to be altered. According to the Code, in Latin names, -å should be transcribed as -ao-. Other transcriptions (-aa- or -a-), however, are preferable to some Scandinavians (see Friis & Thulin 1984: 671). This illustrates the folly of trying to formulate the universal standardization of such things, especially by retro-active legislation.

the reasons. Discussion, however, has persisted concerning the validity of Forskål's names (Heine 1968; Burdet & Perret 1983; Jeffrey 1985) and the question of *E. roka* has been raised again by Friis (1984), whose intention was to end this controversy once and for all, and whose detailed and independent enquiry led to conclusions which are virtually identical to those of Dandy. Friis (1983) has also explained why Forskål's names have been the source of so much trouble.

Dandy's reasons for rejecting *E. roka* are the most convincing yet expressed and it would seem appropriate to publish them here in full — if only as an example of the kind of expertise which is necessary in order to establish the correct names of plants.

The following is taken from a letter dated 11 July 1963 sent by Dandy to Dr L.E. Codd, who was then Director of the Botanical Research Institute, Pretoria, where the original is filed in the herbarium under *T. emetica*.

'Dear Dr Codd,

I am not surprised to have your letter concerning *Elcaja roka*. This 'name' (like *Cornus gharaf* on the same page of Forskål) has been misleading botanists for some time. White consulted me about it for Flora Zambesiaca, and it was after our joint investigation that he reverted to the name *Trichilia emetica*.

I have studied Forskål's *Flora Aegyptiaco-arabica* pretty closely in connexion with the Sudan flora. Like so many works of its period, in the early days of binomial nomenclature, it has its peculiarities; and these are intensified by the fact that the book was published posthumously from Forskål's manuscripts, so that it inevitably suffers from inconsistency and lack of finish.

The plan of the work is that the Flora itself (consisting of systematic floristic lists for the regions concerned) is contained in pages I–CXVI, and it is these lists which give what may be described as Forskål's intended (official) nomenclature. The lists include localities, vernacular names, etc. but usually no descriptions. Descriptions of the new and more interesting plants are given in the second part of the book ('Descriptiones' pp. 1–220), and it is in this part that the new genera, like *Elcaja*, are defined. The treatment here, for the reason already stated, is uneven. Sometimes the species under the new genera are given a binomial, sometimes not; but in the latter cases the missing binomial is usually supplied in the floristic lists (pp. I–CXVI) and is of course validly published by reference to the later part of the book.

In the case of *Elcaja*, however, it so happens that the binomial is missing in both places, and this led Chiovenda to take up *Elcaja roka* from p. XCV. This 'name' appears with a lot of others in lists of plants of medicinal and other importance which Forskål prefaces to his actual floristic lists.

Now if these preliminary lists of species are closely examined (instead of glanced at) it immediately becomes obvious that the 'names' used are not necessarily binomials. Some of the names, especially of common Linnaean species, are, it is true, binomials.

But others are just generic names or generic names followed by vernacular names, and if these species are looked up in the systematic parts of the book it will be seen that Forskål has already provided a binomial for most of them. From p. XCV, where *Elcaja roka* appears, we have the following examples:-

*Cacalia edchera* = *C. odora* pp. CXIX, 146  
*Amyris abu-scham* = *A. opobalsamum*, pp. CX, 79  
*Cornus gharaf* = *C. sanguinea*, pp. CC, 33  
*Thymus dousch* = *T. pulegioides?* p. CXIV  
*Keura kadi* = *K. odorifera*, pp. CXXII, 172  
*Tagetes benefsidj* = *T. dubia?*, p. CXX  
*Cynanchum march* = *C. pyrotechnicum*, pp. CVIII, 53  
*Ficus mudah* = *F. religiosa*, pp. CXXIV, 180

From all this it is evident that in these preliminary lists Forskål is referring to the species by any convenient designation, either by binomial or by vernacular name, and that his 'official' names are those given in the floristic lists. Perhaps if Forskål had completed his manuscript he would have brought all his references into line.

In my opinion, therefore, none of the 'names' listed by Forskål in his preliminary lists is to be regarded as a new binomial. If these 'names' were to be accepted as binomials then all (not just *Elcaja roka*) would have to be so treated and this would lead to absurd results. The fact that *Elcaja*, evidently by accident, failed to receive a binomial in the two botanical parts of the book does not justify the taking up of *Elcaja roka* as the 'missing' binomial.

For the above reasons I consider that the name *Trichilia emetica* Vahl should stand.

Kind regards,  
 Yours sincerely,  
 (Sgd) E. Dandy  
 Keeper of Botany,  
 British Museum (Nat. Hist.).'

*The differences between T. emetica and T. dregeana*

For most of this century taxonomists dealing with the flora of southern Africa failed to distinguish *T. dregeana* from *T. emetica*, though some field workers were well aware of their differences (e.g. the late Prof. A. W. Bayer pers. comm.). Both species are, or were formerly, of considerable economic importance and are frequently referred to collectively in the literature under *T. emetica* or *T. roka*. It is often impossible to know for certain which species is meant. Acocks (1975) for instance only mentions *T. emetica*, though the references on pp. 14, 19, 20 and 26 would appear to apply to *T. dregeana*.

In *Flora Zambesiaca*, White & Styles (1963: 298–302) set out the differences between these species for the first time, and were able to distinguish them using a combination of characters — shape of fruit and shape of leaflets, and for the latter nervation, indumentum and colour when dry. It was pointed out that most of these characters occasionally break down but that if they are all used together most specimens can easily be identified. De Wilde (1968), however, believed that leaflet shape and indumentum are of 'no value at all'. These different

conclusions possibly reflect a difference in approach. In taxonomy, like should always be compared with like. White & Styles specifically mention cases where atypical material fails to show diagnostic characters but they do not sufficiently stress the importance of excluding such material from keys and diagnoses, assuming that this was widely understood and was normal practice. Further work has shown that, if legitimate comparisons are made, there is no difficulty in distinguishing these two species. The following comparisons deal with *T. dregeana* and *T. emetica* only in southern Africa. It is in this part of their range that their distributions interdigitate most intimately and they come into closest contact. It is here that the need for critical comparison is greatest. In general, *T. dregeana* is a species of moist forest and *T. emetica* occurs in riparian forest or various types of 'savanna' in drier regions. In coastal Kenya, however, *T. emetica* occurs in the canopy of quite luxuriant moist forest. Here, in the shape of its leaflets, but not in other respects it is atypical. This, of course, does not necessarily weaken the specific distinctions in other parts of its range, nor indeed in

general, but such variation, *unless carefully handled*, may appear to do so.

(1) *Structure of the fruit and inflorescence*: the most important difference between *T. emetica* and *T. dregeana* is in the shape of the fruit. In the former there is a distinct stipe (Figure 6); in the latter there is none. At first sight this feature seems trivial, but it is correlated with other features of the structure of the inflorescence and infructescence and may be related to the precise way in which the arillate seeds are displayed and presented to the animals which disperse them. For a more general discussion of this theme see Pannell & White (in press).

In *T. dregeana* the female inflorescence is few-flowered and lax and occurs in the axils of well developed leaves. Normally only one fruit matures in each inflorescence, occasionally up to three.

In *T. emetica* the flowers are borne in dense, contracted panicles up to 50 mm long. Each inflorescence has c. 20 flowers. The pedicels are very short and the flowers are almost touching. The inflores-

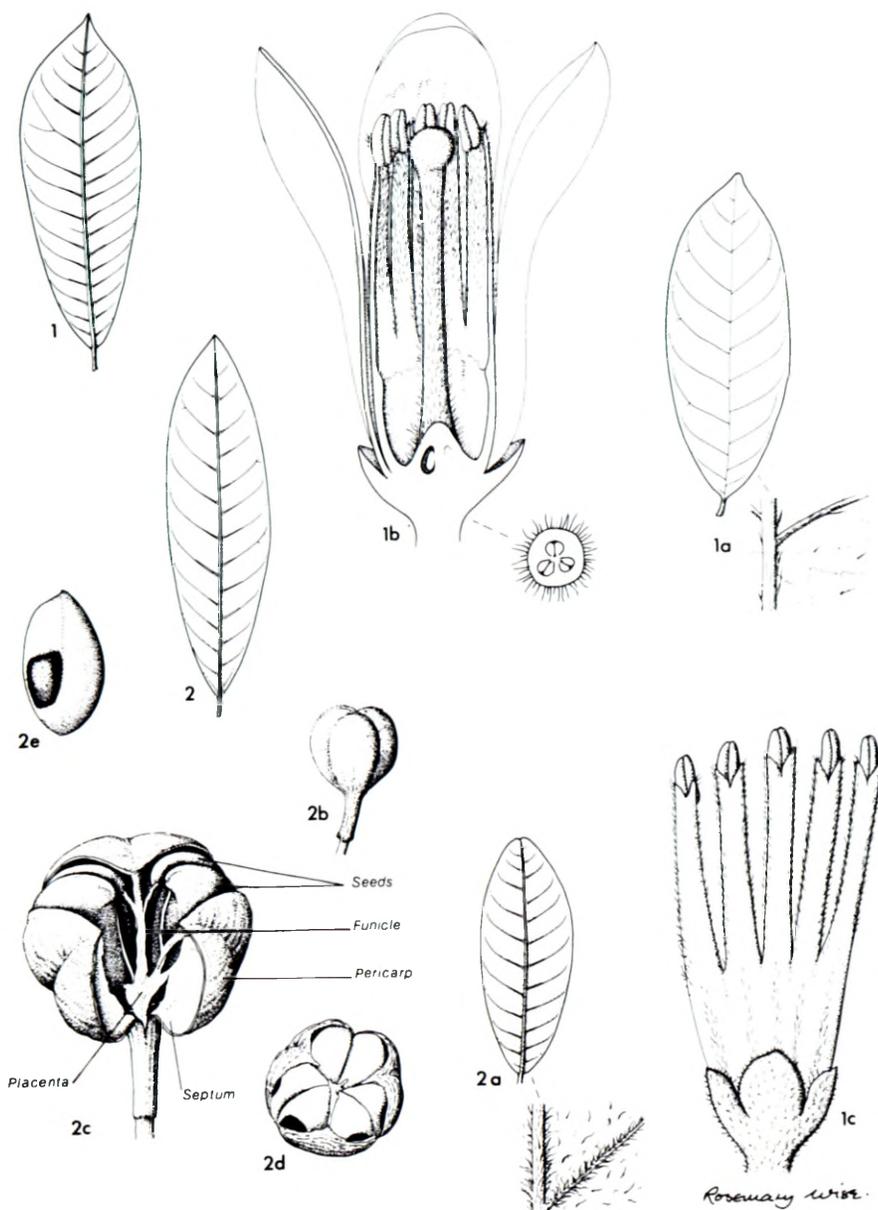


FIGURE 6. — 1. *Trichilia dregeana*, leaflet,  $\times 0.4$  (from Thorns 5348); 1a, leaflet,  $\times 0.4$  and part of lower leaf surface,  $\times 1.8$  (both from Strey 5340); 1b, flower in longitudinal section and ovary in transverse section (both  $\times 2.8$  and from Styles 333); 1c, calyx and androecium,  $\times 2.8$  (from Styles 333). 2. *Trichilia emetica*, leaflet,  $\times 0.4$  (from Liengme 577); 2a, leaflet,  $\times 0.4$  and part of lower leaf surface,  $\times 1.8$  (both from Compton 31147); 2b, unopened capsule,  $\times 0.4$ ; 2c, capsule just beginning to dehisce,  $\times 1.4$ ; 2d, dehiscent capsule viewed from above,  $\times 0.9$ ; 2e, seed,  $\times 1.4$  (all from Bond s.n.).

cences occur singly in the axils of leaves which are separated by internodes less than 20 mm long or are crowded in the axils of reduced foliage leaves which are mostly caducous and form a terminal compound inflorescence about 100 × 80 mm. Several fruits in each inflorescence normally ripen (phot. on p. 120 of Van Wyk 1972) and the stipe performs the function of a pedicel. The less crowded fruits of *T. dregeana* have no need for this. The ripe but undehisced fruit of *T. dregeana* is 30–50 mm in diameter; that of *T. emetica* usually less than 25 mm.

A comparative study of seed dispersal in these two species would be useful.

(2) *Leaflet shape and indumentum*: no difficulty is encountered in identifying specimens of *T. emetica* and *T. dregeana* using leaflet characters alone, though, because of variation, it is not possible to express the differences concisely in words. They can, however, easily be conveyed by illustrations. Figure 6 illustrates two lateral leaflets from the distal half of the leaf of *T. dregeana* (*Strey 5340*, *Thorns 5348*) and two of *T. emetica* (*Compton 31147*, *Liengme 577*). It is the shape of the apex that is significantly different and can be described as follows:-

Apex of lateral leaflets shortly and acutely acuminate or bluntly subacuminate (with the tip itself often shallowly notched), nearly always showing a hollow curve .....	<i>T. dregeana</i>
Apex of lateral leaflets rounded, emarginate or broadly acute, without a hollow curve .....	<i>T. emetica</i>

In this comparison like is compared with like. If terminal leaflets of *T. emetica* are compared with lateral leaflets of *T. dregeana* the distinction is weakened in that the leaf apex of the former sometimes shows a hollow curve.

The differences given above seem to hold for all southern African material with mature undamaged leaves. All the specimens (149 gatherings) of these two species that were available for study in the National Herbarium Pretoria, were compared with the four specimens mentioned above. A good match was found in each case, except for 12 which were unsuitable for comparison in that they lacked well-preserved apices or represented the juvenile condition. In *T. dregeana* the apex of the leaflet sometimes fails to develop normally, possibly due to insect damage or mechanical injury. Such specimens are rare and should not be used in formal taxonomy. One of them (*Scheepers 1042*) is illustrated by De Wilde (1968, fig. 3Aa); another is *White 14126b* (FHO). It was collected from a young 5 m tall tree growing in the garden of Cornelius Grobbelaar in Pretoria, and was the only leaf of its kind. All the other leaves (exemplified by *White 14126a*) on this tree were normal and were a good match for *Strey 5340*.

In southern Africa *T. dregeana* and *T. emetica* are consistently different in the indumentum of their leaves. Figure 6.

(3) *Other differences*: The leaves of *T. dregeana* usually dry brown (not olive-green) and the leaflets often have fewer lateral nerves. The flowers are nearly always larger. All of these characters show

some overlap, though they are frequently useful in identification.

Chromosome counts are few but a wide difference has been reported (Styles & Vosa 1971: *T. dregeana*:  $2n = \pm 360$ ; *T. emetica*:  $2n = 50$ ).

#### *The subspecies of T. emetica*

De Wilde (1968: 50) recognizes two subspecies which are almost completely allopatric, overlapping only in Uganda. Subsp. *emetica* extends from Ethiopia and the Yemen to South Africa. Subsp. *suberosa* De Wilde, which differs in its corky bark, more deciduous habit and somewhat laxer inflorescence, occurs from Senegal to Uganda.

#### *Distribution and ecology of T. emetica and T. dregeana*

Both species are chorological transgressors since they occur in several of the regional phytochoria of the Unesco/AETFAT/UNSO Vegetation Map of Africa (White 1983a). Despite its wide distribution, *T. dregeana* is fairly uniform in its ecology. White (1978a) has referred to it as an ecological and chorological transgressor, but it might be better to re-classify it as a sub-Afromontane near-endemic species (see below). In its ecology *T. emetica* is much more varied.

*T. emetica* extends from Senegal to Ethiopia and southwards to about the latitude of Durban, penetrating inland as far as the Caprivi Strip and north-eastern Botswana. There is an outlying population in the Yemen. In west Africa (subsp. *suberosa*), it is apparently rare (at least in Nigeria) and its characteristic habitat is Sudanian woodland (White 1983a: 105), especially on rocky hills. On the eastern side of Africa it is one of the most characteristic trees of riparian forest, especially where the rainfall is less than 1 000 mm p.a. (White 1983a: 91, 117). In the Zambezi Region it is also found in woodland and wooded grassland on the more fertile soils (White 1983a: 95,96). In the east African coastal belt *T. emetica* is locally an important constituent of semi-evergreen forest as a pioneer species and where the canopy is not too dense. On the Kenya coastal plain it invades fire-protected, secondary wooded grassland with abundant *Hyphaene compressa* H. Wendl. and, because of its rapid growth, it soon overtops the palms. Also in Kenya, *T. emetica* occurs frequently as a 20–25 m tall tree in the rather light canopy of *Combretum schumannii* Engl. forest on coral limestone. It regenerates freely inside the forest (White, MS 1975).

In northern Natal, *T. emetica* is found in riparian forest and locally, as in the Hluhluwe Game Reserve, in scrub forest on rocky slopes. From Mtunzini northwards it is found in various types of coastal forest, both as a pioneer, and in the canopy where the latter is no more than 12 m or so high.

*T. dregeana* is widespread in tropical Africa, but shows major disjunctions between west and east Africa, both north and south of the equator. It is almost confined to upland areas. In South Africa, however, near Maputa and southwards from the Tugela River mouth to its southern limit near the

mouth of the Bashee River, it descends almost to sea level. In west Africa it appears to be confined to a few upland massifs from Guinea to Cameroun, occurring between 800–1 600 m.

On the eastern side of Africa it has a scattered distribution from Ethiopia to South Africa. It chiefly occurs in rain forest and related types on the moister slopes of mountains, but usually at somewhat lower altitudes than typical Afromontane vegetation. Thus in Malawi it occurs between 650 and 1 600 m. It is a characteristic member of mid-altitude rain forest in which typical Afromontane species and lowland species intermingle (White, Dowsett-Lemaire & Chapman, 'The evergreen forest trees and shrubs of Malawi', in prep.). It has not been recorded in Malawi from what White (1983a) calls Afromontane rain forest (the submontane rain forest of Chapman & White 1970), but it occurs very locally in lowland rain forest towards its upper altitudinal limits as in Mpita Forest, the lower slopes of Mt Mulanje and in the Malawi Hills. To the north of Malawi most records are from medium altitudes though it ascends to 1 900 m in Ethiopia and 2 100 m in Uganda (De Wilde 1968).

In Zambia, *T. dregeana* occurs very locally in riparian forest in the higher-rainfall areas. In Angola it is found in the Dembos cloud forest (White & Werger 1978) between 800 and 1 000 m. *T. dregeana* also occurs near Luki and Temvo in Bas Zaire between 200 and 500 m. In view of its consistently submontane character elsewhere in tropical Africa, these low-altitude occurrences are puzzling. They are not without parallel, however. *Nuxia congesta*, for example, an Afromontane near-endemic species, locally has small satellite populations at low altitudes, e.g. near the mouth of the Zaire River (Leeuwenberg 1975; White 1983b: Fig. 4a).

In southern Africa it occurs in forest in the mountains of the NE Transvaal. Scheepers (1978) records it from *Cussonia spicata* Thunb., *Ficus sur* Forsk. kloof forest between 1 125 and 1 200 m in the Submontane scrub forest belt and from climax *Trichilia dregeana*, *Cussonia spicata*, *Cryptocarya liebertiana* Engl. forest between 1 200 and 1 250 m in the Montane forest belt. In both these types Afromontane and lowland forest species intermingle and they are clearly related to the mid-altitude forests of Malawi and elsewhere further north.

Further south in Natal and the Transkei, *T. dregeana* is predominantly a lowland species which locally, as in Komgha District, ascends to  $\pm$  570 m. It is a characteristic member of Tongaland-Pondoland lowland forest (White 1983a: 199) and has been recorded from eight out of the 15 stands for which quantitative information is available (Moll & White 1978: 580). In these forests, and in others for which there are floristic records, e.g. Ngoye (Huntley 1965 as '*emetica*') and Umtamvuma Nature Reserve (White 1973, MS) Afromontane species, such as *Calodendrum capense* (L.F.) Thunb., *Drypetes gerardii* Hutch., *Kiggelaria africana* L., *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb., *P. latifolius* (Thunb.) R. Br. ex Mirb., *Rapanea melanophloeos* (L.) Mez and *Xymalos monospora* (Harv.) Baill.,

occur, though lowland species are much more abundant. North of Mtunzini, *T. emetica* appears to replace *T. dregeana* in coastal forest on the leeward side of dunes and in their hinterland. *T. dregeana* however occurs in seasonal swamp forest at the headwaters of the Sihadla River near Maputo (White 10475).

#### Habit

Both species develop wide umbrageous crowns when growing in the open. In southern Africa, *Trichilia emetica* rarely exceeds 12 m in height but can exceed 20 m in east Africa.

The maximum height of *T. dregeana* south of the Limpopo seems to be 20 m. In Malawi it can reach twice that size. When growing in the forest it develops a long straight bole and relatively narrow crown no wider than the height of the tree (photo in Palmer & Pitman 1972). In 1940 the famous Thunder Tree in Mitchell Park, Durban, though less than 20 m high, had developed a crown nearly twice that diameter. The bole which was 5.5 m across was branched at about 2 m and supported massive wide-spreading limbs. The tree was said to have made no appreciable increase in size during the previous 50 years (A. P. D. McClean in litt. 19 Jan. 1940, in PRE; Cuthbertson 1950, as '*emetica*').

#### Fruit structure and dispersal

In *T. dregeana* and *T. emetica*, as the capsule opens the placenta breaks up and its dismembered parts remain attached to the separating valves. If both ovules in a locule develop, each seed resembles a somewhat distorted segment of an orange; they have two flat sides and one outer curved surface. That side which is in contact with the 'sister' seed is larger and flatter than the opposite one which is appressed to the septum. The outer surface is hence asymmetric. The red aril covers the whole seed except for a patch on the outer face where the black testa is exposed. When the capsule begins to open, this black 'eye' is hidden, but as the valves continue to separate it frequently becomes visible.

Frost (1980) records eight species of bird as eating the arils of *T. emetica* at Mtunzini in Natal. There are no comparable records for *T. dregeana* from South Africa. In Malawi it is eaten by *Onychognathus walleri* starlings (F. Dowsett-Lemaire, unpublished).

### 7. PSEUDOBERSAMA Verdc.

*Pseudobersama mossambicensis* (Sim) Verdc. in Journal of the Linnean Society, Botany 55: 504, fig. 1; White & Styles: 305, fig. 60 (1963). Type: Mozambique, without locality, *Sim 5204* (not located); fig. 23 in Sim (1909), lectotype here designated.

*Bersama mossambicensis* Sim: 34, fig. 23 (1909).

#### Typification

Neither Verdcourt nor White & Styles succeeded in locating the type, and it has not subsequently come to light. Sim re-numbered many of his specimens and his collection was divided between several herbaria. The only Sim specimen that I have seen

(PRE 21178) is possibly part of the original material though it is not a very good match for Sim's rather sketchy illustration. As Verdcourt has said the latter is unmistakable. In these circumstances it seems that Sim's figure should be designated as a lectotype (Art. 7.4).

#### *Distribution and ecology*

*P. mossambicensis* has a scattered distribution in coastal forest from Kenya to Natal, and is therefore a Zanzibar Inhambane/Tongaland-Pondoland linking species, or east African coastal endemic. In southern Africa it is only known from a few forests in northern Tongaland where it is locally a common canopy tree (Tinley 321).

#### *Fruit structure and dispersal*

*P. mossambicensis* is unique in the family in having a woody capsule which is massive in its construction in relation to the small arillate seeds contained in it. It seems that the plant is using much more of its resources for protecting the developing seed than for attracting and 'rewarding' its dispersers (Pannell & White 1985). Nothing, however, is known of the reproductive biology of this species. When more is known, *P. mossambicensis* might provide clues to the evolution of wind-dispersed Meliaceae such as *Entandrophragma*.

### 8. ENTANDROPHRAGMA C. DC.

A genus of 11 species. Six species, namely, *E. angolense* (Welw.) C. DC., *E. candollei* Harms, *E. congoense* (De Wild.) A. Chev., *E. cylindricum* (Sprague) Sprague, *E. palustre* Staner and *E. utile* (Dawe & Sprague) Sprague, occur in the Guineo-Congolian rain forest region. *E. excelsum* (Dawe & Sprague) Sprague is an Afromontane rain forest species. There are three Zambesian endemics or near-endemics: *E. caudatum* (Sprague) Sprague, *E. deveoyi* De Wild. and *E. spicatum* (C. DC.) Sprague. The remaining species, *E. bussei* Harms, which is related to, but distinct from, *E. spicatum* occurs only at and immediately adjacent to the southern extremity of the Somalia-Masai region.

The rain forest species emerge above the canopy and are among the tallest of African trees. The other species, though shorter, also emerge from the drier types of forest, woodland and thicket in which they occur. All species produce mahogany. That of *E. utile*, known in the timber trade as 'Utile' is highly esteemed. The southern African species are too rare to be of commercial importance, and in common with the other species have not been successfully grown in plantations.

*Entandrophragma* is unique among southern African Meliaceae in having wind-dispersed, winged seeds. Nothing is known about the mechanism of dispersal. In Nigeria the seeds of *E. angolense* are shed towards the end of the dry season but several weeks before the rains break. The five valves are shed leaving the seeds packed along each face of the central column. They stay like this for a week or more until a sudden gust of wind liberates them when they rotate as they fall to the ground. Few are

carried far beyond the parent tree and most are destroyed by predators, especially mice. Some, however, travel considerable distances and saplings have been found up to 0,8 km from the nearest tree from which the seeds could have come (J. D. Chapman in Pannell & White 1985).

In the southern African species dispersal is presumably broadly similar but the details of seed liberation are different. The capsule dehisces from the apex (see Figure 19 in White & Styles (In press, a) and other illustrations cited therein) and the valves move outwards but remain firmly attached to the base of the capsule which now looks like a shuttlecock. The seeds, however, remain firmly attached to the columella, and presumably they also are liberated by the action of strong wind.

#### 1. *Entandrophragma caudatum* (Sprague) Sprague in Kew Bulletin 1910: 180 (1910).

This species is confined to the southern part of the Zambezi Region, except for a slight intrusion into the northern part of the Tongaland-Pondoland Region. It is not very variable. One specimen (*De Winter 7737* from near Louis Trichardt) is unusual in having leaflets broadly cordate or hastate at the base. The leaves, however, are not attached and may have come from a young plant.

#### 2. *Entandrophragma spicatum* (C. DC.) Sprague in Hooker's Icones Plantarum 31: in nota sub fig. 3023 (1915).

This species is confined to a small area at the eastern extremity of the Zambezi Region and extends into the Zambezia/Kaokoveld-Mossamedes transition (White 1983: 191) which connects the Zambezi and Karoo-Namib Regions. Other Zambezi species, e.g. *Colophospermum mopane* (Kirk ex Benth.) J. Léonard (Figure 12 in Volk 1966) extend to the fringes of the Mossamedes-Namib desert in this region of abrupt climatic gradients.

### DISCUSSION

#### *Chemistry and the taxonomy of the Meliaceae*

##### (a) Introduction

According to Harborne & Turner (1984), taxonomy, thirty five years ago, entered a new Biochemical phase (p. 36). The purpose of their book is to review up to the end of 1982 the state and potential of this approach to plant systematics (p. viii). To judge from their 'philosophical and pragmatic rationale' (as summarized on p. 45 and from statements made elsewhere) they equate taxonomy with phylogeny, and make insufficient distinction between descriptive and historical biology. Although they refer (p. 33) to the importance of gross morphology at the present time, they imply that chemistry will ultimately prove to be more important. In concluding a chapter on the application of chemistry at the family level in a section which deals with secondary metabolites they say that 'it appears obvious that chemical approaches both micromolecular and macromolecular will soon yield a classificatory bulwark which is likely to withstand the whim and whine of any number of newly inspired intuitional

workers using the long-overworked, now classical, megamorphic approaches' (p. 312), whatever that may mean. Elsewhere (p. 291), they say that 'secondary compounds are primarily useful in taxonomic studies at the species and generic level'.

I believe that Harborne & Turner underestimate both the achievements and potential of the traditional approach, and that their particular advocacy is, at best, premature and may never be substantiated. Recent work on the Meliaceae suggests that, in that family at least, secondary compounds are more useful at higher taxonomic levels than at genus and species level.

#### (b) Limonoids and the Meliaceae

Although much work remains to be done, the secondary compounds of the Meliaceae have probably been as thoroughly studied during the last 25 years as any predominantly tropical family of comparable size and diversity. Work on the taxonomy and chemistry was done independently though the principal investigators have maintained close contact. Some tentative historical interpretations are emerging from the taxonomy (Pannell & White, in press) but the primary aims so far have been to delimit and describe taxa as objectively as possible, and to study their ecology.

Chemically, the Meliaceae is characterized by the presence of limonoids, a group of oxidized triterpenes. According to Taylor (1984) more than 250 limonoids have been extracted and identified from 54 species belonging to 23 genera. Limonoids have been found to occur in nearly every member of the family so far investigated. Elsewhere, they are only known from *Harrisonia abyssinica*, currently placed in Simaroubaceae, a few Rutaceae, and Cneoraceae, three families usually placed in the same order as Meliaceae. Of these families the Meliaceae is the most diverse in its limonoid profile. In their limonoid chemistry the members of the Meliaceae collectively form an extremely tightly knit and sharply defined group.

#### (c) The position of *Ptaeroxylon* and *Nymania*

The inclusion of both genera in the Meliaceae has been questioned. Both were examined for limonoids. *Ptaeroxylon* (see p. 144) was found to lack them, so confirming its exclusion from Meliaceae, on other grounds, by Leroy (1959, 1960) and White & Styles (1966). By contrast, *Nymania* does have limonoids (p. 145) and White (present study), after an independent assessment of previous work, accepts these chemical findings as an additional reason for including it in Meliaceae. *Nymania* is a genus of special interest. In its leaves, flowers and fruits it looks most un-meliaceous and it is easy to understand why some South African botanists want to exclude it. On visual inspection it seems to have little in common with other South African members of the family, but its distinctive features can largely be explained by its ecology. Ecologically, it is one of the most specialized genera in the family. It is a bird-pollinated, semi-desert xerophyte with wind-dispersed capsules. When it is studied in relation to the ecological, chorological and morphological patterns of the family as a whole its membership is seen to be more

convincing. Its chemistry seems to clinch the matter of its inclusion, but provides no clues about its closest relatives. Its limonoids belong to a group which is widely distributed in the family. The decision to place it in a unigeneric tribe next to Turraeae was taken on grounds other than chemistry.

#### (d) Southern African *Trichilia*: chemistry and the taxonomist's eye

In herbarium taxonomy, when preserved material is sparse and field experience limited, mistakes are often made, but they are easily rectified as knowledge increases. This was so for *Trichilia emetica* and *T. dregeana* (p. 158). Now that they have been shown to differ, everyone recognizes them, both in the field and in the herbarium. Their distinctive features are discussed and illustrated in the present account, in which it is shown that, provided comparisons are carefully made, identification is easy. When the specific differences are known it is possible to classify herbarium specimens as quickly as they can be handled, that is, in effect, instantaneously. Identification in the field is not more difficult (J. D. Chapman; I. Friis pers. comm.; F. White pers. obs.). On the other hand there is no evidence to suggest that these two species are not very closely related. Phytochemical evidence superficially appears to be at variance, though to a chemist with a knowledge of the structures of the compounds concerned, there may be a simple explanation (D. A. H. Taylor in litt., 26 February 1986).

Taylor (1984) has classified the limonoids of Meliaceae into 10 groups based on an increasing degree of oxidation. *T. emetica* is placed in group 2, the Havanensis Group alongside *Azadirachta*, *Khaya*, *Melia*, *Toona* and *Turraea*, to mention only those genera which are indigenous or cultivated in southern Africa. *T. dregeana* has limonoids in groups 9 and 10; both groups include *Toona* and *Nymania*.

#### (e) Conclusions

Limonoid chemistry is compatible with the way the family has been circumscribed using traditional means. But within the family the distribution of the different classes of limonoids is not always closely correlated with morphology. The reasons for this are under investigation (Taylor, Pannell, Styles & White, in prep.), though there are no indications that, for Meliaceae at least, the traditional approach to taxonomy is in danger of being superseded. There are, however, some indications that a deeper knowledge of limonoid chemistry would increase ecological understanding. This subject, however, remains largely unexplored.

#### *Taxonomy as a visual art*

It was said above that in some circumstances plant species can be identified 'by eye' with great rapidity. If this were not so, the great masters of the past, on whose labours present-day and future taxonomy is founded, could not have been so productive. Pictorial representation in taxonomy, however, with some notable exceptions, is insufficiently used. In White & Styles (In press, a) every species has been illustrated in sufficient detail to make identification possible. The text merely draws attention to and

elaborates on the main differences between taxa, and provides additional historical and biological information.

For two species, *Ekebergia capensis* and *Turraea obtusifolia*, complex patterns of geographical variation are depicted by means of pictorialized distribution maps (Figures 3 & 5). Although this method has been in use for more than 30 years, it is rarely resorted to and many published accounts of taxonomically difficult complexes are impossible to understand because of its lack. In my experience the pictorialized distribution map can often display the evidence on which taxonomic judgement should be based, more effectively than any other means.

*The Meliaceae and the chorology of southern Africa*

The Meliaceae has many more species and is much more diverse in lowland tropical rain forest than in any other type of vegetation. Presumably, it underwent most of its differentiation there. In common with some other predominantly tropical rain forest families, e.g. Fabaceae: Caesalpinioideae, it is also well represented in drier types.

Most of southern Africa lies outside the tropics and there is little rain forest. Both in Australia, which is situated at similar latitudes, and in South Africa very restricted taxa occur as well as species

which are very widely distributed in the tropics to the north. The distributions in southern Africa of all species indigenous there, are indicated on Figure 7 and on Figure 8 which also record distribution in relation to the phytochoria of White (1983a). There are five types of distribution:

(a) two species, *Entandrophragma spicatum* and *Turraea zambesica*, are confined to the tropics, but only occur towards its southern limits;

(b) five species, *Nymania capensis*, *Turraea pulchella*, *T. streyi*, *T. obtusifolia* and *Ekebergia pterophylla*, lie wholly or predominantly outside the tropics. The first three are taxonomically very isolated;

(c) *Entandrophragma caudatum* occurs mostly inside the tropics but only in the southern part of the Zambezi Region;

(d) *Pseudobersama mossambicensis* is confined to the forests of the east African coastal belt;

(e) the remaining species, *Ekebergia capensis*, *Trichilia dregeana*, *T. emetica*, *Turraea floribunda* and *T. nilotica* are widespread in Africa and occur in several phytochoria.

A diverse pattern like the one summarized above confirms the need for a flexible, non-hierarchical chorological framework such as that used for the

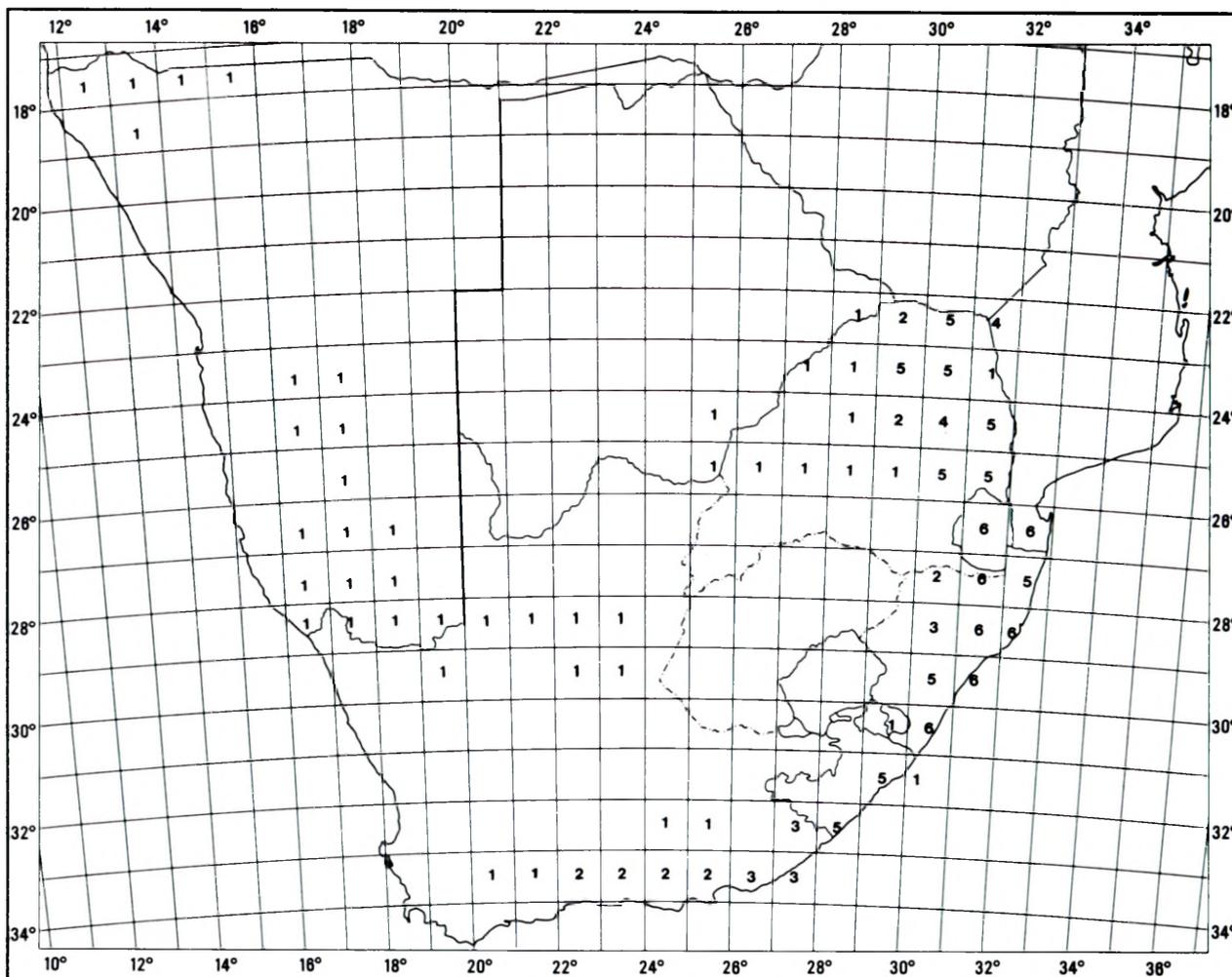


FIGURE 7. — Density map of Meliaceae in southern Africa showing the total number of species in each degree square.

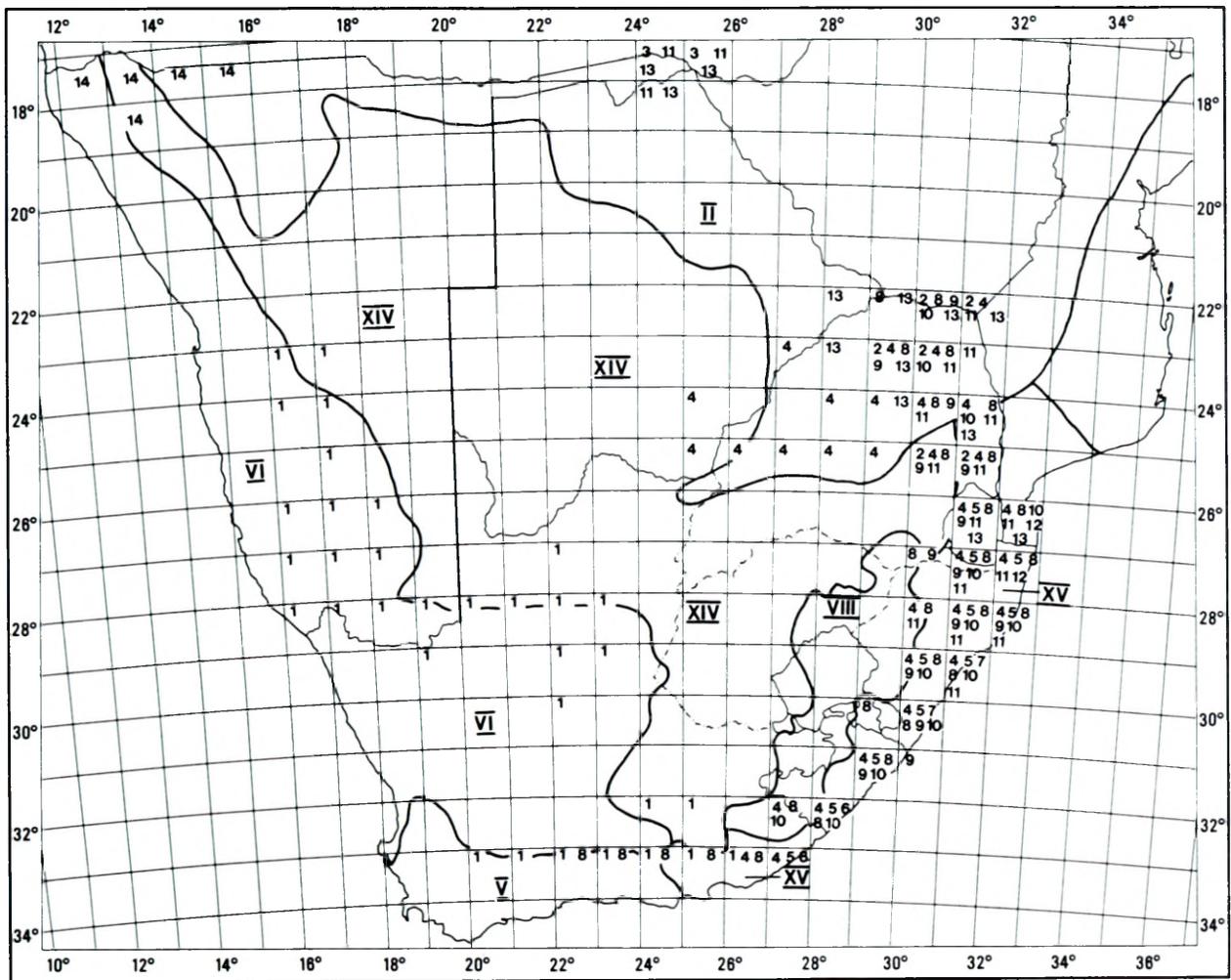


FIGURE 8. — Map of Meliaceae in southern Africa showing the occurrences of the 14 indigenous species in each degree square and the approximate boundaries of the regional phytochoria of White (1983a). II, Zambebian regional centre of endemism; V, Cape regional centre of endemism (enclaves of Karoo and Afromontane vegetation not shown); VI, Karoo-Namib regional centre of endemism; VIII, Afromontane archipelago-like regional centre of endemism; XIV, Kalahari-Highveld regional transition zone; XV, Tongaland-Pondoland regional mosaic. 1, *Nymanina capensis*; 2, *Turraea nilotica*; 3, *T. zambeziaca*; 4, *T. obtusifolia*; 5, *T. floribunda*; 6, *T. pulchella*; 7, *T. streyi*; 8, *Ekebergia capensis*; 9, *E. pterophylla*; 10, *Trichilia dregeana*; 11, *T. emetica*; 12, *Pseudobersama mossambicensis*; 13, *Entandrophragma caudatum*; 14, *E. spicatum*.

AETFAT Vegetation Map of Africa. For some purposes at least, this approach seems preferable to 'simple areal definitions' such as that adopted by Goldblatt (1978: 375) for the Cape Floristic Region, notwithstanding some obvious administrative advantages of the latter. A special feature of the AETFAT system is that the distinctness of the great regional centres of endemism is enhanced by the recognition of regional transition zones, and regional mosaics of complex chorological affinity. For the Cape Region the exclusion of large enclaves of non-fynbos vegetation serves a similar purpose. Southern African Meliaceae illustrate this theme. Thus:

(a) the Kalahari-Highveld Transition Zone has no endemic Meliaceae but two species cross its limits as marginal intruders;

(b) the chorological heterogeneity of the Tongaland-Pondoland Mosaic is confirmed by the occurrence of: (i) two endemic species of *Turraea* (*T. pulchella* and *T. streyi*) of limited geographical extent which comprise a very distinct section; (ii) two Tongaland-Pondoland near-endemic species (*Ekebergia pterophylla*, *Turraea obtusifolia*) which extend a

short way into the Zambebian Region; (iii) one marginal intruder (*Pseudobersama mossambicensis*) from the Zanzibar-Inhambane Region; (iv) one marginal intruder (*Entandrophragma caudatum*) from the Zambebian Region; (v) one marginal intruder (*Nymanina capensis*) from the Karoo-Namib Region; and (vi) four chorological transgressors (*Ekebergia capensis*, *Trichilia dregeana*, *T. emetica*, *Turraea heterophylla*);

(c) the distribution of *Nymanina capensis* supports the practice of restricting the Cape Region to areas dominated by fynbos and related types of vegetation and excluding from it extensive enclaves of forest, bushland and Karoo (see Figures 1 & 2).

#### The function of taxonomic characters

Taxonomy is improved when function is understood; and historical interpretation (when it is possible at all) can be approached with greater confidence when we know how organisms 'work' and interact. In the conventional, museum-based approach to taxonomy, differences between related taxa are frequently expressed in stereotyped terms (e.g. 'fruit

dehiscent or indehiscent') which may conceal a multitude of differences. The latter are liable to escape detection until the importance of ecology in taxonomy is realized. This has been convincingly shown by the work of Hopkins (1983, 1984) on the pantropical bat-pollinated genus *Parkia* (Fabaceae: Mimosoideae) and of Pannell & Koziol (in press) on the Far Eastern bird- and primate-dispersed genus *Aglaia* (Meliaceae). In several places in the foregoing account both the potential significance and our ignorance of the ecology of southern African Meliaceae has been pointed out, particularly in relation to pollination and dispersal. I hope that South African botanists will regard this as a challenge to discover more about their living flora. They may need the collaboration of zoologists but the subject is too important to be left to zoologists alone.

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