Taxonomic revision of the *Memecylon natalense* species-complex in southern Africa

by

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PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Biology School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville, South Africa. The research was financially supported by the National Research Foundation and the Botanical Educational Trust.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

Signed: Dr Syd Ramdhani

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DECLARATION 1: PLAGIARISM

I, Imercia Gracious Mona, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

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(a) their words have been re-written but the general information attributed to them has been referenced;

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DECLARATION 2: PUBLICATIONS

My role in each paper is indicated. The * indicates corresponding author.

1. Mona, I.G.,* Stone, R.D., 2016. Morphometric analysis and taxonomic revision of the *Memecylon natalense* species-complex (Melastomataceae) in southern Africa. South African Journal of Botany 103, 334. [Conference Abstract]
https://doi.org/10.1016/j.sajb.2016.02.11
Contribution - I contributed to the writing of the abstract, mini oral and poster presentation at the South African Association of Botanists meeting held in January 2016.

2. Stone, R.D.,* Mona, I.G., Ramdhani, S., 2017. Revised treatment of Mozambican *Memecylon* (Melastomataceae—Olisbeoideae), with descriptions of four new species in *M.* section *Buxifolia*. Phytotaxa 331, 151–168.
https://biotaxa.org/Phytotaxa/article/view/phytotaxa.331.2.1/30718
Contribution - I contributed to the morphological analyses and species descriptions, and together with the other two authors we all contributed substantially to the writing of the manuscript.

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ABSTRACT

Two *Memecylon* species (*M. natalense* and *M. bachmannii*) were previously recognized in southern Africa, and three species of *M.* section *Buxifolia* as occurring in Mozambique (*M. natalense, M. torrei* and *M. insulare*). However, a recent nrDNA phylogeny revealed that *M. natalense* as previously circumscribed is not a monophyletic group and includes some geographically outlying populations warranting recognition as distinct evolutionary lineages. In this dissertation, I present the results of a comprehensive morphological study and revision of the '*M. natalense* species-complex' including the following taxa: *M. natalense* sensu stricto (endemic to South Africa in KwaZulu-Natal, Eastern Cape, Mpumalanga and Limpopo), *M. incisilobum* (southern Mozambique), *M. nubigenum* (southern Malawi), *M. rovumense* (southeastern Tanzania), *M. aenigmaticum* (northern Mozambique), *M.* sp. nov. 1 (northeastern Kwazulu-Natal, South Africa), *M.* sp. nov. 2 (Eastern Cape province, South Africa), and *M.* sp. nov. 3 (Limpopo province, South Africa). Although *M. bachmannii* (Eastern Cape and KwaZulu-Natal) is morphologically distinct, it was also included in the present study because of recent nrDNA work indicating a close relationship with *M. natalense*. Species boundaries were investigated using phenetic and cladistic methods based on morphology. Phenetic analysis using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) revealed that *M. bachmannii* clustered independently, *M.* sp. nov. 1 clustered close to *M. incisilobum*, *M. aenigmaticum* clustered close to *M. rovumense,* and *M. nubigenum* clustered close to a subcluster consisting of *M. natalense, M.* sp. nov. 2 and *M.* sp. nov. 3. The morphological cladistic results were congruent with a previous molecular analysis in that *M.* sect. *Buxifolia* was monophyletic. *Memecylon rovumense* + *M. aenigmaticum* and *M. incisilobum* + *M.* sp. nov. 1 appeared in separate clades. *Memecylon bachmannii* and *M. nubigenum* were each monophyletic, while *M. natalense*, *M.* sp. nov. 2 and *M.* sp. nov. 3 appeared in an unresolved polytomy. Overall, the cladistic results were in agreement with the UPGMA analysis but were less resolved. Vegetative and fruit morphology have proven to be of great diagnostic value in delimiting the members of the *M. natalense* species-complex. Four new species have been named and described, while a further three new species are proposed. Dichotomous keys are provided, and the conservation status of each species is assessed according to the criteria of the

IUCN. A lectotype should be designated for *M. natalense*. With these additions, the flora of Mozambique now has seven species of *Memecylon* (including six species in *M.* sect. *Buxifolia*). In South Africa, the number of recognized *Memecylon* species has increased from two to five.

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CHAPTER 1: INTRODUCTION

1.1. Background

Memecylon L. is a paleotropical, species-rich genus (Stone, 2014) that belongs to Melastomataceae Juss., one of the largest flowering plant families in the world (Renner, 1993; Conti et al., 1997; Clausing and Renner, 2001). Members of this genus are small to medium-sized trees or understory shrubs, commonly occurring in tropical evergreen forests (Stone, 2014). Economically, *Memecylon* is poorly explored, however, in tropical Asia the genus is of particular interest due to its distinctive ornamental flowers, edible fruits, timbers, dye and medicinal properties (Bharathi et al., 2016). The Indian-Sri Lankan species *M. umbellatum* Burm. f. has the most reports on the above-mentioned uses (Sivu et al., 2013; Bharathi, et al., 2016).

In South Africa (SA), *M. natalense* Markgr. and *M. bachmannii* Engl. are the only two *Memecylon* species previously recognized (Van Wyk, 1983; Coates-Palgrave, 2002; Germishuizen et al., 2006; Boon, 2010). The species of interest in this project is *M. natalense*, a small tree mostly 2–6 m in height, occurring in the understory of evergreen (Coates-Palgrave, 2002) or Afromontane forests (Schmidt et al., 2002). It is sporadically distributed in the Eastern Cape and KwaZulu-Natal (KZN) provinces, with some outlying populations in Mpumalanga and Limpopo provinces (Coates-Palgrave, 2002). According to the *Flora Zambesiaca* (Fernandes and Fernandes, 1978), the range of *M. natalense* also extends to northern Mozambique and southern Malawi. Southern Africa refers is to a geographical region not to the smaller area treated by the *Flora of Southern Africa*, which includes only South Africa, Namibia, Lesotho, Botswana and Swaziland

Recent molecular studies (Stone, 2014; Stone et al., 2017a) have clearly shown that some outlying *Memecylon* populations in southern Africa are genetically distinct from *M. natalense*. These genetically distinct populations include the Mt Mulanje population in southern Malawi, the Soutpansberg population in Limpopo, as well as two coastal populations in north-eastern KZN (near Kosi Bay) and southern Mozambique (Gaza province near Praia do Bilene) which are genetically identical to each other but quite distinct in comparison to *M. natalense.* Based on these results, *M. natalense* as previously circumscribed was considered to include some populations better regarded as separate, semi-cryptic species (Stone et al., 2017a).

Bickford et al. (2007) defined cryptic species as two or more distinct evolutionary lineages that have been classified as one due to close morphological similarity. The study of cryptic species is of great significance in the field of taxonomy and also benefits other disciplines, such as evolutionary theory, biogeography and conservation planning (Bickford et al., 2007). Moreover, with the increasing worldwide destruction and disturbance of natural ecosystems, catastrophic extinctions of species are accelerating (Brooks, 2006). If these cryptic species are not captured in our Linnaean system of classification they will continue evade detection (Schlick-Steiner et al., 2007). Given that many plant species remain undescribed, we might be losing even more species than we expected. Thus, efforts to catalogue and explain biodiversity need to be prioritized, and this is not feasible without precise documentation of species (Sangster, 2009).

1.2. Family placement and generic delimitation of *Memecylon*

Memecylon was first established by Linnaeus (1753) in his artificial grouping of *Octandria monogynia*. Shortly thereafter, it was placed in family Onagraceae by Jussieu (1789). Du Petit-Thouars (1811) was the first to include *Memecylon* in Melastomataceae. Don (1823) later excluded *Memecylon* from Melastomataceae to be in Myrtaceae using mainly anther characteristics and leaf nervation. While Blume also (1826-1827) preferred to treat *Memecylon* as a member of Myrtaceae.

de Candolle (1827) established a separate family Memecylaceae DC. to include *Memecylon* and *Mouriri*. Some later authors supported this circumscription (Gardner, 1840; Lowry, 1976; Dahlgren and Thorne, 1984), while others supported the expansion of Melastomataceae to include *Memecylon* (Chamisso, 1836; Lindley, 1836, 1846; Naudin, 1852; Cogniaux, 1891). Based on morphological and anatomical character analysis, Renner (1993) recognised Melastomataceae and Memecylaceae as separate families, with Memecylaceae circumscribed to include *Memecylon*, *Mouriri*, *Votomita* Aubl., *Spathandra* Guill. & Perr., *Lijndenia* Zoll. & Moritzi and *Warneckea* Gilg.

Molecular analyses of cpDNA sequences by Clausing and Renner (2001) supported the treatment of Memecylaceae and Melastomataceae *sensu stricto* as sister-groups, but a recent analysis by Stone (2006) treated *Memecylon* within the subfamily Olisbeoideae Burnett (an older name for subfamily. Memecyloideae Meisner), and recognised this group as one of four Melastomataceae subfamilies. Currently, *Memecylon* and the other memecyloid genera are still included in the Melastomataceae *sensu lato* (Angiosperm Phylogeny Group [APG], 2009).

Following the monographic treatment of Cogniaux (1891), it was customary to treat the monospecific African genus *Spathandra*, the paleotropical *Lijndenia* and the African-Madagascan *Warneckea* as synonyms of *Memecylon sensu lato*. It was much later, after careful morphological and anatomical studies, that *Spathandra*, *Warneckea* (Jacques- Félix, 1978a) and *Lijndenia* (Bremer, 1982) were re-established as separate genera, and *Memecylon* was circumscribed to exclude these genera. The concepts of these segregate genera are further supported by phylogenetic analyses of the nuclear *GapC* gene (Stone, 2006) and nuclear ribosomal DNA spacers (Stone, 2014). According to the maximum-likelihood analysis of Stone (2006), *Warneckea* is the sister-group of *Lijndenia* and *Spathandra* is the sister-group of *Memecylon*.

Characters deemed to be important in delimiting these genera are: mid-ribbed leaves, filiform sclereids, and an embryo with wrinkled cotyledons and a long hypocotyl in *Memecylon*; 3-ribbed leaves, spheroidal foliar sclereids, and an embryo with single fleshy cotyledon in *Warneckea*; 3-ribbed leaves, reniform or polyramous foliar sclereids, an embryo with rolled cotyledons and short hypocotyls in *Spathandra*; and strongly trinervate to multinervate, papillose-muricate leaves (the distinctive texture owing to the presence of ramiform sclereid idioblasts in the mesophyll) in *Lijndenia* (Bremer, 1982). Collectively these three genera are readily distinguished from *Memecylon sensu stricto* by their ± strongly trinervate or multinervate leaves (Stone, 2014). The obscurely acrodromous leaf nervation of *Memecylon sensu stricto* has been interpreted as a loss of the strongly trinervate condition (Jacques-Félix, 1995; Stone 2006).

1.3. Infrageneric classification of African *Memecylon*

Engler (1921) described *Memecylon* sect. *Polyanthema* Engl., sect. *Tenuipedunculata* Engl., sect. *Cauliflora* Engl. and sect. *Obtusifolia* Engl. Later, Jacques-Félix (1978a, 1978b, 1979, 1983a, 1983b) recognised sect. *Mouririoidea* Jacq.-Fél., sect. *Polyanthema* Engl., and sect. *Afzeliana* Jacq.-Fél. The sections *Cauliflora* and *Obtusifolia* were treated as taxonomic synonyms of sect. *Polyanthema*, and sect. *Tenuipedunculata* was not recognised.

Stone (2014) elevated *Memecylon* sect. *Mouririoidea* to subgeneric rank and narrowed the circumscription of sect. *Polyanthema* to comprise only the members of the "*M. polyanthemos* complex" sensu Jacques-Félix (1979). Engler's (1921) sections *Tenuipedunculata*, *Cauliflora* and *Obtusifolia* were re-instated, and sect. *Afzeliana* was retained. Within subgenus *Memecylon*, seven new sections were proposed, namely: sect. *Buxifolia* R.D. Stone, sect. *Diluviana* R.D. Stone, sect. *Felixiocylon* R.D. Stone, sect. *Germainiocylon* R.D. Stone, sect. *Magnifoliata* R.D. Stone, sect. *Montana* R.D. Stone, and sect. *Sitacylon* R.D. Stone.

Memecylon sect. *Buxifolia* is a monophyletic group that was circumscribed to include ten species (*M. amplifolium* R.D. Stone, *M. bachmannii*, *M. buxifolium* Blume, *M. fragrans* A. Fern. & R. Fern., *M. insulare* A. Fern. & R. Fern., *M. multinode* Jacq.-Fél., *M. myrtilloides* Markgr., *M. natalense*, *M. torrei* A. Fern. & R. Fern., and *M. verruculosum* Brenan [Stone, 2014]). In addition, four new Mozambican species were recently described and added to this section (*M. incisilobum* R.D. Stone & I.G. Mona, *M. nubigenum* R.D. Stone & I.G. Mona, *M. rovumense* R.D. Stone & I.G. Mona and *M. aenigmaticum* R.D. Stone [Stone et al., 2017b]), making a total of 14 species. The overall range of sect. *Buxifolia* is from East Africa (Kenya and Tanzania in coastal and Eastern Arc forests) southwards to the eastern part of SA and disjunctly in the dry forests of western and northern Madagascar (Stone, 2014). The section is diagnosed by the combination of branchlets with successive nodes alternating between normal leaves and reduced, often inflorescence-bearing bracts, white petals with corolla rounded to apiculate in bud, and anther connectives bearing a dorsal oil-gland. Amongst the other sections of East African *Memecylon*, an anther gland is found only in the Tanzanian *M.* sect. *Magnifoliata* R.D. Stone which differs in its cauliflorous habit and ellipsoid to obovoid fruits, while *M.* sect. *Obtusifolia* Engler is characterized by its unusually thick bark, yellowish green leaves and subdeltate-acuminate petals (Stone, 2014).

1.4. Taxonomic history of South African *Memecylon*

1.4.1. *Memecylon natalense*

The original description of *Memecylon australe* Gilg & Schlechter (in Schlechter, 1907) was based on a specimen (*Rudatis 149*) in the Berlin herbarium which was later destroyed during World War II (Merrill, 1943; Hiepko, 1987). However, an isotype of the same collection was re-discovered in the Paris Museum (Van Wyk, 1983). Below is the protologue of *Memecylon australe* Gilg & Schltr. (in Schlechter, 1907), translated from the original Latin:

Many-branched shrub or erect tree 3–4 m high. Branches and branchlets sparsely leafy, glabrous, slightly quadrangular towards the apex. Leaves short-petioled, elliptic, apex acute, base cuneate, glabrous on both abaxial and adaxial surfaces, texture leathery, only the midrib visible, lateral nerves entirely obscure, blades about 2.5–3.6 cm long × 0.8–2 cm wide, yellow on lower surface. Cymes axillary, few-flowered, peduncles and pedicels short, glabrous. Calyx cupuliform, glabrous, slightly and obtusely 4-lobed. Petals rhomboid-rounded, subacute, glabrous, barely 0.4 cm long. Stamens longer than the petals, filaments very slender, glabrous, anthers obtuse, curved at the base, glabrous. Style subfiliform, glabrous, ± equalling the length of the stamens. Hypantho-calyx obconic, glabrous.

When the original description of *M. australe* was published, it was in fact an illegitimate later homonym of *M. australe* C. Moore (in Moore and Betche, 1893), an entirely different species currently known as *Acmena australis* (C. Moore) L.A.S. Johnson (family Myrtaceae). Later, Markgraf (in Mildbraed, 1934) proposed the replacement name *M. natalense* Markgr. for the South African species originally described as *M. australe* Gilg & Schltr.

Later, Fernandes and Fernandes (1972, 1978, 1980) expanded the circumscription of *M. natalense* to include not only the material from South Africa but also some collections from southern Malawi (Mt Mulanje) and northern Mozambique.

1.4.2. *Memecylon bachmannii*

Memecylon bachmannii first appeared in a key to the species of *M.* sect. *Polyanthema* (Engler, 1921). According to the available description, this species agrees with the protologue of *M. grandiflorum* A. Fern. & R. Fern. (Fernandes and Fernandes, 1955), a species endemic to the same localities as *M. bachmannii* [southern KwaZulu-Natal and Pondoland (Eastern Cape)] clearly indicating that these names apply to the same species. Hence, according to the rule of priority Art. 11.4 (Turland et al., 2018), Van Wyk (1983) proposed that the earliest legitimate name *M. bachmannii* Engl. is the correct name with *M. grandiflorum* as a taxonomic (i.e. heterotypic) synonym. No specimens were cited in the original description of *M. bachmannii* (Engler, 1921), but the locality and choice of the specific epithet suggest that the species was probably based on material gathered by F.E. Bachmann who visited Pondoland in 1888 (Van Wyk, 1983). Following the loss during World War II of Engler's original material in

Berlin, Van Wyk (1983) further proposed a neotype specimen (*Van Wyk 5318*, PRU) for *M. bachmannii* according to Art. 9.11 (Turland et al., 2018).

Memecylon bachmannii and *M. natalense* are quite distinct from each other at the morphological level, and their identity as separate species has never been questioned. Where their respective geographic ranges overlap in southern KwaZulu-Natal and the Eastern Cape, *M. natalense* tends to occur in somewhat drier habitats. Surprisingly, however, a recent study with population-level sampling (Stone et al., 2017a) found that the nrDNA ITS sequences of *M. natalense* and *M. bachmannii* are identical or nearly so, suggesting that they are recently diverged "ecological species" (Van Valen, 1976) or alternatively that there has been genetic introgression between them following secondary contact. These results, together with those of Stone (2014), suggest that *M. bachmannii* and *M. natalense* are closely related and form a monophyletic group nested within the predominantly East African clade *M.* section *Buxifolia*. Therefore, any attempt to revise the *M. natalense* species-complex must also address its similarities and differences in comparison to *M. bachmannii*.

1.5. Aim of the present study

This study aims to complete a comprehensive taxonomic revision of the *Memecylon natalense* species-complex (including *M. bachmannii*) using morphological data.

1.6. Key objectives

I. To identify taxonomically important characters that can be used for species identification. The study will make use of the "diagnostic species concept", where species are defined as the smallest cluster of organisms possessing at least one diagnostic (i.e. unambiguous) character (Cracraft, 1989).

II. To investigate phenetic groupings (Chapter 3) and cladistic relationships (chapter 4) based on morphological data.

III. To provide a dichotomous key to the species.

IV. To prepare a formal taxonomic treatment, including description and naming of new species according to the rules of botanical nomenclature (Turland et al., 2018). Herbarium acronyms follow *Index Herbariorum* (Thiers, continuously updated)

V. To assess the conservation status of each species according to the criteria of the International Union for Conservation of Nature (IUCN) (2012).

CHAPTER 2: MORPHOLOGY

2.1. Introduction

The study of plant morphology has a long history (Kaplan, 2001). In taxonomy, it plays a vital role in species identification (Sattler, 1991), and remains practically relevant as morphological concepts are not limited to biological sciences but are also useful in other disciplines such a molecular biology and ecology (Sattler, 1991; Sattler and Rutishauser, 1997). Despite the need for multiple lines of evidence including molecular (e.g. DNA) and ecogeographic data (Schlick-Steiner et al., 2010), morphological data are the fundamental source of information upon which plant classification is based **(**MacLeod, 2002).

Memecylon L. is a taxonomically difficult genus because it is not rich in terms of taxonomic characters. Additionally, the flowers are small, the basic floral morphology is rather highly conserved, and flowering events are rarely observed, making it necessary to use vegetative features in classification (Stone, 2014). This is certainly true of the semi-cryptic taxa of the *M. natalense* species-complex of Mozambique and SA (Mona and Stone, 2016). This chapter discusses in detail the morphological characters used in the taxonomic treatments presented later in this study (see Chapter 5 & 6).

Taxa in the present investigation include:

I. Two previously recognised South African species:

- *Memecylon natalense* Markgr.
- *Memecylon bachmannii* Engl.

II. Four recently described Mozambican species (Stone et al., 2017b):

- *Memecylon incisilobum* R.D. Stone & I.G. Mona, a coastal population from Gaza province in southern Mozambique.
- *Memecylon nubigenum* R.D. Stone & I.G. Mona, from mountains of northern Mozambique and southern Malawi.
- *Memecylon rovumense* R.D. Stone & I.G. Mona, from coastal forests in northern Mozambique (Cabo Delgado province) and southern Tanzania (Lindi Region).

- *Memecylon aenigmaticum* R.D. Stone from northern Mozambique (Cabo Delgado).

III. Three new, semi-cryptic South African species:

- *Memecylon* sp. nov. 1, a coastal population from Kosi Bay Nature Reserve in northeastern KZN province.
- *Memecylon* sp. nov. 2, a small-leaved population from the Dwesa-Cwebe and Hluleka Nature Reserves in Eastern Cape (EC) province.
- *Memecylon* sp. nov. 3, an endemic of the Soutpansberg (Limpopo province).

2.2. Material and Methods

Field collections were made for taxa found in KZN and EC provinces. I did my MSc at Westville Campus but I made sure I was able to collect in Umtamvuna (*M. bachmannii*), Nature Reserve (KZN) and along the Ntsubane–Mbotyi road (EC, Lusikisiki district), *M. natalense* from Ongoye Forest (KZN), *M.* sp. nov. 1 from the Sihadla Forest in Kosi Bay Nature Reserve (KZN), and *M.* sp. nov. 2 from Dwesa-Cwebe nature reserves (EC) when necessary. The other taxa under investigation were not visited *in situ* due to logistical and time constraints. Consequently, they were studied based on herbarium specimens housed in the Bews (NU) and Ward (UDW) herbaria, as well as material received on loan from the National Herbarium, Pretoria (PRE), Natal Herbarium (NH), Buffelskloof Nature Reserve Herbarium (BNRH), H.G.W.J. Schweickerdt Herbarium (PRU) and the Royal Botanic Gardens, Kew (K).

2.3. Survey of morphological characters

2.3.1. Habit

All the examined *Memecylon* taxa are woody shrubs or small trees of forest understory habitats (Fig. 2.1). Field notes associated with collections indicate considerable variation in height of individual trees/shrubs. Some taxa have been recorded (or observed) as being small trees (e.g., *M. bachmannii*, 3–4 [–6] m; *M.* sp. nov. 2, 3–4 m), or shrubs (e.g., *M. aenigmaticum*, 3 m; *M.* sp. nov. 3, 2.5–3 [–5] m). Most taxa are small trees to tall trees: *M. natalense*, 2–4 (–15) m; *M. incisilobum*, 7 m; *M. nubigenum*, 4–7(–17) m; *M. rovumense*, 6 m.; *M.* sp. nov. 1, 4–10 (–12) m. It can be concluded that, given suitable habitat conditions and a lack of disturbance (e.g., fire), individual trees have the potential to grow up to 15–17 m high (as seen in *M. natalense* and *M. nubigenum*, respectively). Variation in height of individual trees thus seems to be environmentally determined and is not useful as a taxonomic character. To fully understand the influence of climate and topology conditions on tree height variability, an in-depth field study would be needed.

Figure 2.4. Habit of **A.** *Memecylon bachmannii* (photo by Dr Syd Ramdhani). **B**. *M*. sp. nov. 3 (photo by John Burrows).

2.3.2. Bark

All taxa in this study have similar bark, at least for those collected/observed as trees. The bark is of a greyish-brown colour and has shallow, vertically arranged, closely spaced fissures (Fig. 2.2).

Figure 2.5. Bark of **A.** *Memecylon* sp. nov. 1 (photo by David Styles). **B.** *M*. sp. nov. 3 (photo by John Burrows).

2.3.3. Branchlets

The young branchlets are slender, quadrangular and thickened at the nodes while the older branchlets are terete, longitudinally fissured and have thin white flakes that are shed longitudinally (Fig. 2.3). The young branchlets also have "aphyllous" nodes, i.e. nodes bearing only squamiform leaves that are also floriferous at times (Jacques-Félix, 1983a).

Figure 2.6. Branchlets of *Memecylon* sp. nov. 3 (photos in **A.** and **B.** by John Burrows). Arrows in **B.** point to "aphyllous" nodes.

2.3.4. Leaves

The leaves of all *Memecylon* taxa studied are opposite, simple, entire, and glabrous. The leaf-blades are dark green and glossy above, and paler below. There is a single midnerve which is sunken on the adaxial surface and prominent below, where it is thickest near the petiole and tapering towards the apex. There are 1–2 pairs of lateral nerves that are faintly visible on both surfaces in some taxa (*M. incisilobum*, *M. nubigenum*, *M. rovumense*, *M. aenigmaticum*, *M.* sp. nov. 1), whereas in others the lateral nerves are obscure (*M. natalense*, *M. bachmannii*, *M.* sp. nov. 2, *M.* sp. nov. 3). Characters pertaining to leaf texture, shape, base and apex has a strong diagnostic value among the *Memecylon* taxa included in this study.

2.3.4.1. Leaf texture

Leaf texture may be thinly coriaceous (*M. natalense*, *M. bachmannii*, *M. rovumense*, *M.* sp. nov. 2, *M.* sp. nov. 3), sub-coriaceous (*M.* sp. nov. 1, *M. incisilobum*, *M. nubigenum*) or thickly coriaceous (*M. aenigmaticum*).

2.3.4.2. Shape of leaf-blade

There is great variation in leaf shape and dimensions (Table 2.1), including suborbicular (*M. bachmannii*, *M.* sp. nov. 2), broadly ovate (*M. natalense*, *M.* sp. nov. 2, *M.* sp. nov. 3), ovate (*M. nubigenum*, *M rovumense*), elliptic (*M. nubigenum*, *M. incisilobum*, *M.* sp. nov. 1) or obovate (*M. aenigmaticum*) (Fig. 2.4). The *M. natalense* populations from KZN, EC and Mpumalanga has mostly broadly elliptic-ovate to broadly ovate leaves while the Wolkberg population in Limpopo having narrowly elliptic leaves. Collections of *M.* sp. nov. 2 from the Cwebe Nature Reserve have broadly ovate to suborbicular leaves like those of *M. bachmannii* and also broadly elliptic-ovate leaves like those of *M. natalense*. Variation in leaf shape is also observed in *M. rovumense* (ovate to elliptic or obovate).

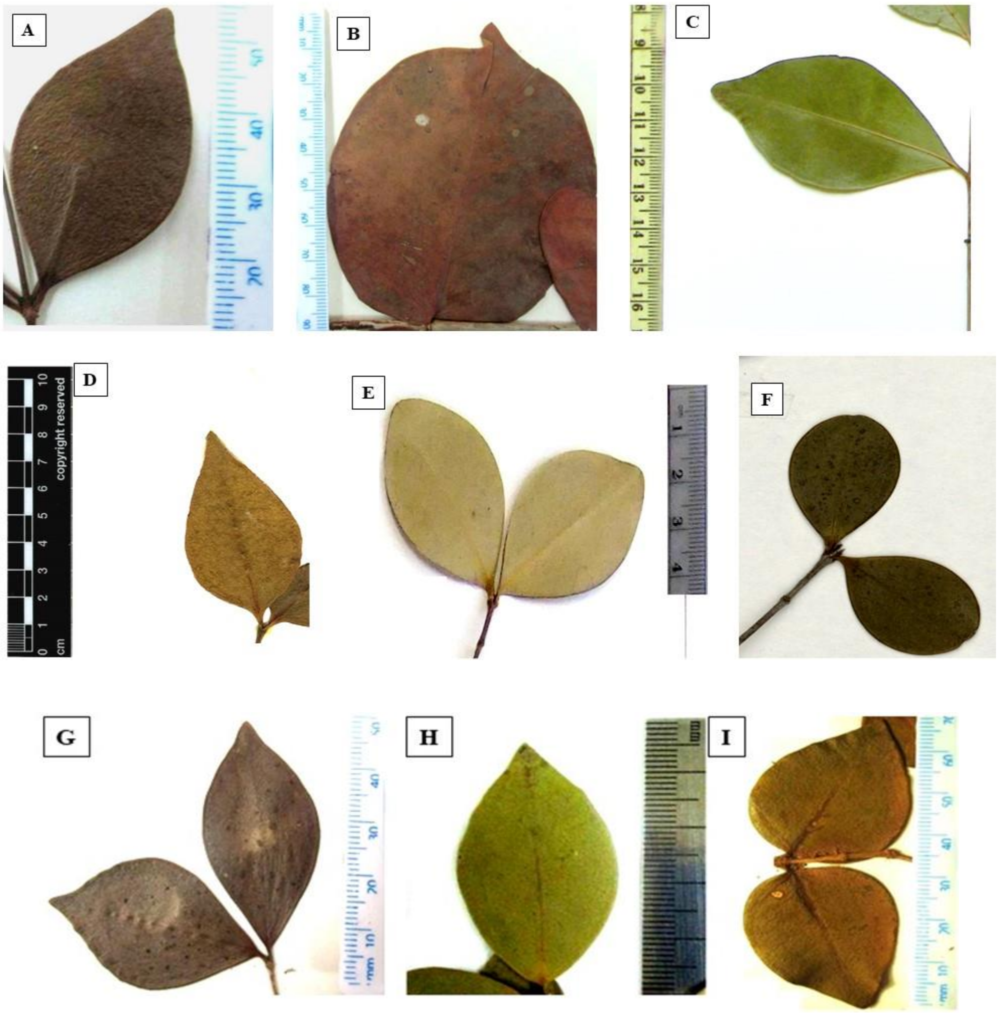


Figure 2.4. Leaf shapes shapes of *Memecylon* taxa. **A.** *M. natalense* (*Van Wyk 7332*, PRU). **B.** *M. bachmannii* (*Strey 5888*, PRE). **C.** *M. incisilobum* (*Burrows 11512*, NU; photo by Dr R. D. Stone). **D.** *M. nubigenum* (*Torre & Correia 16431*, K). **E.** *M. rovumense* (*Clarke 56*, K). **F.** *M. aenigmaticum* (*Timberlake et al. 5574*, K; photo by Dr R. D. Stone). **G.** *M.* sp. nov. 1 (*Stone 2795*, NU). **H.** *M.* sp. nov. 2 (*Stone 2802*, NU). **I.** *M.* sp. nov. 3 (*Van Wyk 4075*, PRU).

Table 2.1. Summary of leaf shape and dimensions for Mozambican and South African *Memecylon* taxa.

Taxon	**Leaf shape**	**Leaf dimensions**	
		Length (mm)	Width (mm)
M. natalense	Elliptic or broadly ovate	(14–) 30–50 (–60)	15–30 (–40)

M. bachmannii	Suborbicular & broadly ovate	40–90 (–100)	30–50 (–65)
M. incisilobum	Elliptic	(45–) 50–70 (–85)	(18–) 25–35 (–45)
M. nubigenum	Ovate to ± elliptic	(25–) 35–50 (–60)	(12–) 18–25 (–32)
M. rovumense	Elliptic to ± ovate or obovate	(25–) 35–55 (–70)	(13–) 18–33 (–40)
M. aenigmaticum	Obovate	17.5–30	10–17.5
M. sp. nov. 1	Elliptic to obovate	(30–) 40–60 (–80)	(12–) 18–30 (–38)
M. sp. nov. 2	Broadly ovate, elliptic broadly ovate	35–45 (–55)	(25–)30–35 (–40)
M. sp. nov. 3	Ovate to broadly ovate	(25–) 30–45 (–55)	(18–) 20–35

2.3.4.3. Base shape

The shape of the leaf base varies from rounded and shallowly cordate (*M. bachmannii*; Fig. 2.5) to cuneate (*M. natalense*, *M. incisilobum*, *M. nubigenum*, *M. rovumense*, *M. aenigmaticum*, *M.* sp. nov. 1). In *M.* sp. nov. 2, the shape varies from cuneate to rounded, and in *M.* sp. nov. 3 from shallowly cordate to obtuse or cuneate (also see Fig. 2.4).

Figure 2.5. Shallowly cordate leaf base of *Memecylon bachmannii* (*Strey 5888*, PRE).

2.3.4.4. Apex shape

The shape of the leaf apex also varies among taxa (see Fig. 2.4). These shapes include acutely acuminate (*M. natalense*), abruptly short-acuminate (*M. bachmannii*), acute (*M. nubigenum, M.* sp. nov. 2, *M.* sp. nov. 3), obtuse (*M. nubigenum*), obtusely acuminate (*M. incisilobum*, *M. rovumense*, *M.* sp. nov. 1), or rounded (*M. aenigmaticum*). Variation is seen among populations of *M. natalense*; in Mpumalanga province, the leaf apices are longer than average (about 10 mm versus 2–4 mm elsewhere) (Fig. 2.6).

Figure 2.6. Leaf apex of *Memecylon natalense* from Mpumalanga province (*Burrows 8936*, BNRH).

2.3.4.5. Petiole

In all *Memecylon* taxa studied, the petioles generally range from 0.5–3 (–4) mm in length (Fig. 2.7). In colour they are yellowish green, and usually grooved on the upper surface. However, in *M. bachmannii*, *M* sp. nov. 2 and *M.* sp. nov. 3 the petioles tend to be very short (0.5–1 mm long and dorsoventrally compressed (or the leaves could be described as subsessile, in sharp contrast to *M. natalense*, *M. incisilobum*, *M. nubigenum*, *M. rovumense*, *M. aenigmaticum* and *M* sp. nov. 1 whose leaves always have distinct petioles). Aside from differences in length, the petioles have no other distinguishing characteristics.

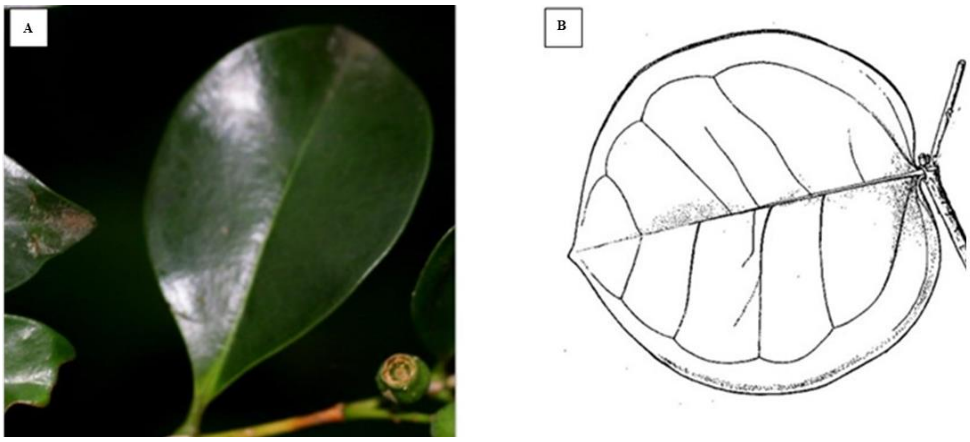


Figure 2.7. Variation in petiole length. **A.** Distinct petiole of *Memecylon* sp. nov. 1 (photo by David Styles). **B.** Subsessile leaf of *M. bachmannii* ×1 (line drawing of *Galpin 9568*, PRE; reproduced from Fernandes and Fernandes, 1955).

2.3.5. Inflorescence

The *Memecylon* taxa in this study generally have a cymose inflorescence (Fig. 2.8) borne at the defoliated nodes of older branchlets, less often in the leaf axils and at the aphyllous nodes alternating with those bearing fully developed leaves. In *M. aenigmaticum*, the inflorescence and floral characters have not been studied since there was only one fruiting specimen available for this study. However, the axis of the infructescence is very short (ca. 2 mm). The inflorescence of *M. aenigmaticum* is most likely similar to that of *M. rovumense*, in which the material thus far available has fruits and floral buds but no open flowers.

Figure 2.8. Cymose inflorescence of *Memecylon incisilobum* (photo by John Burrows).

2.3.5.1. Peduncle

The peduncle sometimes appears jointed because of deciduous bracteoles present at these positions. The length varies among taxa, ranging from 1.5–2 (–3) mm (*M. natalense*, *M. bachmannii*, *M. rovumense*, *M. aenigmaticum*, *M.* sp. nov. 2), to (0.5–) 3–5 (–6.5) mm (*M.* sp. nov. 1), and 4–10 (–13) mm (*M. incisilobum*, *M. nubigenum*, *M.* sp. nov. 3). The peduncles of *M. bachmannii* and *M.* sp. nov. 2 are dorsoventrally compressed and very short, i.e., 0.5–1 (–2) mm; this character distinguishes these two taxa from the others.

2.3.5.2. Secondary axes

The secondary axes (measured to exclude the peduncle) generally vary from 2–7 mm long. However, in *M. rovumense* the secondary axes are ± absent and the flowers are thus directly subumbellate.

2.3.5.3. Bracteoles

The flowers of *M. bachmannii* and *M.* sp. nov. 2 are closely subtended by three pairs of persistent, opposite-decussate bracteoles (Fig. 2.9), and this character separates these two taxa from the others in this study (in which the bracteoles are rapidly deciduous and thus not seen).

The lowermost pair of bracteoles are keeled on the back, 2.5 × 2 mm in *M. bachmannii* and (0.5–) 1 × 1.5 mm in *M.* sp. nov. 2. The middle pair of bracteoles is broadly ovate-cordiform and dorsally carinate, 4 × 4 mm in *M. bachmannii* and 2 × 1.5 (–2) mm in *M.* sp. nov. 2. The uppermost pair of bracteoles is concave being 4 × 5.5 mm in *M. bachmannii* and 2 × 3 mm in *M.* sp. nov. 2.

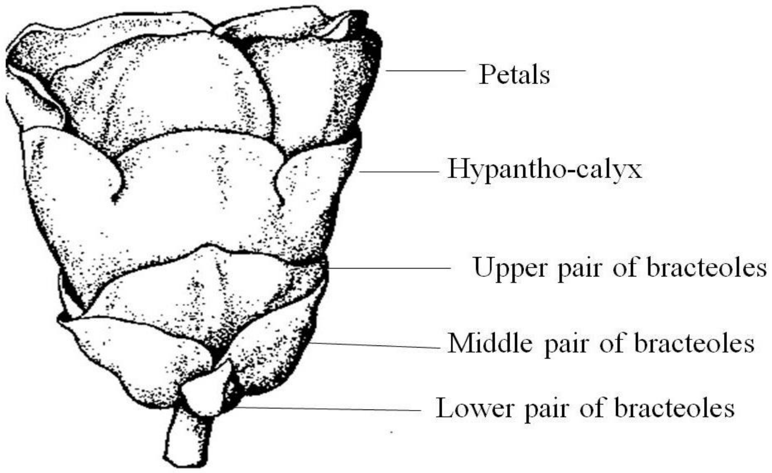


Figure 2.9. Floral bracteoles in *Memecylon bachmannii* ×4 (line drawing of *Galpin 9568*, PRE; reproduced from Fernandes and Fernandes, 1955).

2.3.5.1. Floral buds

In all taxa, the corolla in bud is much longer than the calyx and well exposed. The colour of the corolla is white, except in *M. bachmannii* where it turns dark purple only to become pure white again at anthesis. The corolla shape varies among taxa, ranging from rounded to subacute (*M. natalense*), subacute (*M. nubigenum*, *M. rovumense*, *M.* sp. nov. 3), rounded-apiculate (*M. bachmannii*, *M.* sp. nov. 1, *M.* sp. nov. 2), or sharply apiculate (*M. incisilobum*) (Fig. 2.10).

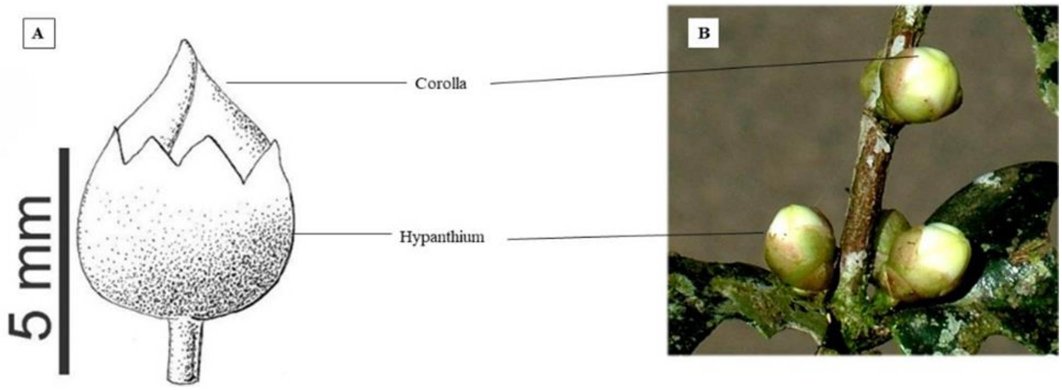


Figure 2.10. Floral buds of **A.** *Memecylon incisilobum* (line drawing of *Burrows 14765*, BNRH; reproduced from Stone et al., 2017b). **B.** *M. bachmannii* (photo by Richard Boon). **C.** *M. bachmannii* (photo by Prabha Amarasinghe). **D.** *M.* sp. nov. 3 (photo by John Burrows).

2.3.5.5. Flowers

Flowers are borne individually at the ends of the inflorescence axes. Flowers are usually 1–3 (–4) in number (except for *M. incisilobum* in which there are up to 9 flowers per cyme).

2.3.5.6. Hypantho-calyx

In all the *Memecylon* taxa under study, the flowers have an expanded, cup-shaped floral tube or receptacle called the hypanthium, bearing near its rim the calyx-lobes, petals, and stamens (Fig. 2.11). The shape of the hypantho-calyx varies amongst the study taxa, including obconic (*M. natalense, M. nubigenum, M.* sp. nov. 1, *M.* sp. nov. 2), cupulo-patellate (*M.* sp. nov. 1), broadly cupuliform (*M. incisilobum*) or campanulate (*M. bachmannii*, *M.* sp. nov. 3).

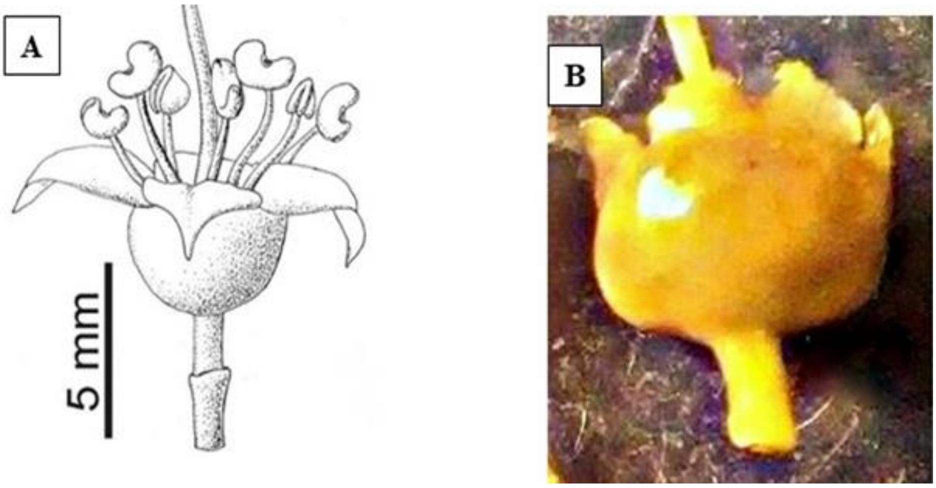


Figure 2.11. **A**, **B.** Hypantho-calyx of *Memecylon incisilobum* (*Burrows 14765,* BNRH; line drawing in **A.** reproduced from Stone et al., 2017b).

The hypantho-calyx is crowned with lobes of different shapes: broadly rounded (*M. incisilobum*, *M. nubigenum*), broadly rounded to triangular (*M. natalense*, *M.* sp. nov. 1, *M.* sp. nov. 3) or broadly rounded to subtriangular (*M. bachmannii*, *M.* sp. nov. 2). The calyx-lobes mostly range in size from 0.5–1 × 0.5–2 mm. In *M. bachmannii* the lobes are slightly larger (1–3 × 2–3 mm). In *M. natalense*, *M. bachmannii,* and *M.* sp. nov. 2 the calyx is distinctly 4-lobed, but in other taxa the lobes are indistinct. In *M. incisilobum* and *M.* sp. nov. 1 the calyx-lobes have a scarious margin that is incised or erose-denticulate, while in the other taxa the lobes are entire. The calyx-lobes of *M. natalense* (e.g., the Ongoye Forest population) are sometimes suffused with dark purple colour, but in other species they remain green or yellowish-green.

2.3.5.7. Petals

The petals are white, 4-merous, symmetric, and glabrous in all the *Memecylon* taxa of this study (Fig. 2.12). Petal shapes vary from rhomboid to rounded (*M. natalense*, *M.* sp. nov. 3), broadly ovate to rhombiform (*M. incisilobum*), or suborbicular (*M. bachmannii, M. nubigenum, M.* sp. nov. 1, *M.* sp. nov. 2). In *M. incisilobum* the petals are keeled on the back. The petal apex is subacute (*M. natalense*, *M. nubigenum*), acuminate (*M. bachmannii*, *M. incisilobum*, *M.* sp. nov. 2), or shortly apiculate (*M.* sp. nov. 1, *M.* sp. nov. 3).

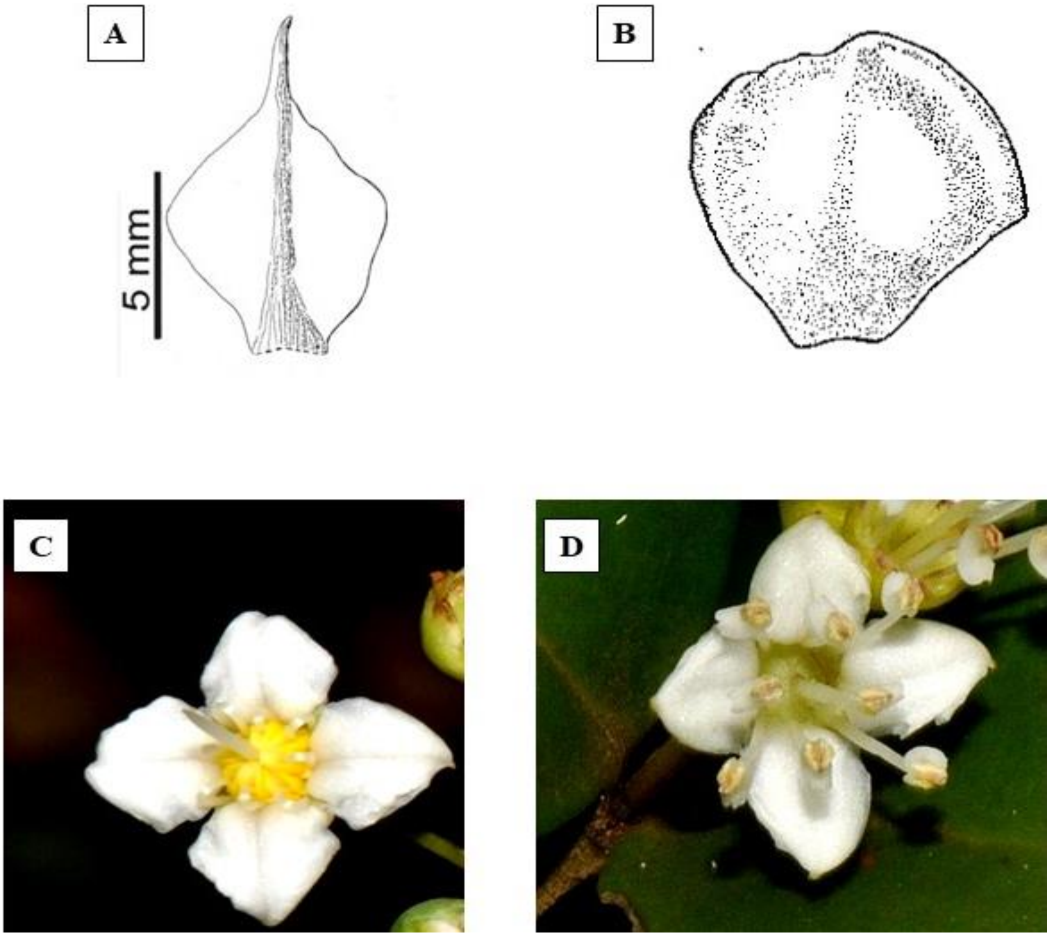


Figure 2.12. Petals of **A.** *Memecylon incisilobum* (line drawing of *Burrows 14765*, BNRH; reproduced from Stone et al., 2017b). **B.** *M. bachmannii* ×4 (line drawing of *Galpin 9568*, PRE; reproduced from Fernandes and Fernandes, 1955). **C.** *M. incisilobum* & **D.** *M.* sp. nov. 3 (photos by John Burrows).

2.3.5.8. Stamens

In *Memecylon* there are 8 ± equal, glabrous stamens borne on flattened filaments ranging in length between (4–) 7–10 mm, and generally longer than the petals (Fig. 2.13). The anthers are dolabriform, medifixed and 2-locular with the locules (thecae) opening by longitudinal slits. The connective is greatly enlarged and strongly incurved by the dorsal oil-gland, with the thecae positioned at the anterior end.

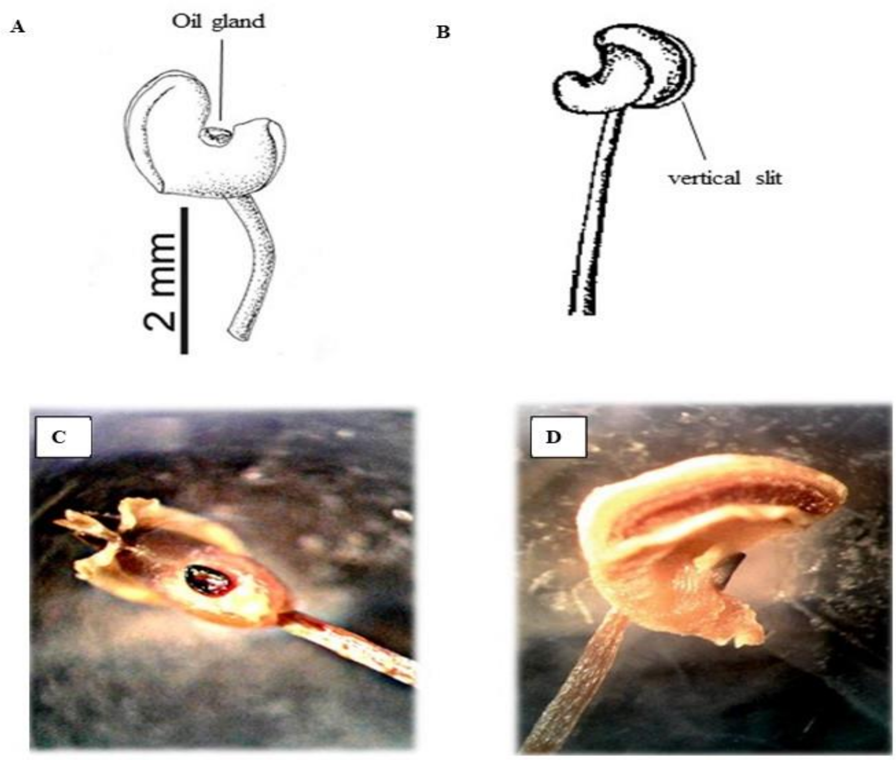


Figure 2.13. Stamens of **A**. *Memecylon incisilobum* (line drawing of *Burrows 14765*, BNRH; reproduced from Stone et al. 2017b). **B**. *M. bachmannii* ×4 (line drawing of *Galpin 9568*, PRE; reproduced from Fernandes and Fernandes, 1955). **C**, **D**. *M.* sp. nov. 3 (*Burrows 13905*, BNRH, K).

During recent field-work it was observed that the colour of the anther connective in *M. natalense*, *M. bachmannii* and *M.* sp. nov. 3 is white, whilst in *M. incisilobum* and *M.* sp. nov. 1 the connective is yellow (Dr R. D. Stone, pers. obs.). In the Madagascan species of *M.* sect. *Buxifolia* the connectives are also yellow, so it is possible that "white connective" is a synapomorphy for the South African clade *sensu lato* Stone et al. (2017a).

2.3.5.9. Style and ovary

The style is glabrous, filiform, and longer than the stamen. Its length ranges between 7−10 mm for all the taxa in this study (Fig. 2.14). The ovary is unilocular with very short free central placentation housing 2–8 ovules (but as many as 12 ovules in *M. bachmannii*). There is little variation in style and placentation among the taxa; and these characters thus have little or no diagnostic value.

Figure 2.14. Style of *Memecylon bachmannii* (photo by Richard Boon).

2.3.5.10. Epigynous chamber

The epigynous chamber is the cupule formed by the interior of the hypanthocalyx. In *Memecylon* (like other Myrtales) the stamens are inflexed in bud, and the anthers rest on top of the ovary, often separated from each other by membranous partitions radiating outwards from the base of the style. In at least three of the study species (*M. natalense, M. nubigenum, M.* sp. nov. 3), the epigynous chamber is smooth (i.e., lacking radial partitions) whilst in *M. incisilobum* there are membranous partitions forming a V-shaped structure beneath each petal and with a low, non-membranous ridge radiating from the base of the style towards each episepalous stamen.

2.3.6. Fruits

The fruits are baccate and 1-seeded. The immature fruits are green in colour, turning dark purple to blackish when ripe. The shape and size of the fruit as well as features of the calycinal crown provide the most reliable diagnostic characters in the taxa under study.

2.3.6.1. Fruit shape

The shape of the fruit varies from subglobose (*M. nubigenum*, *M. incisilobum*, *M.* sp. nov. 1, *M.* sp. nov. 2, *M. bachmannii*) to ellipsoid (*M.* sp. nov. 3, *M. natalense*), broadly pyriform (*M. rovumense*) or obovoid (*M. aenigmaticum*) (Fig. 2.15).

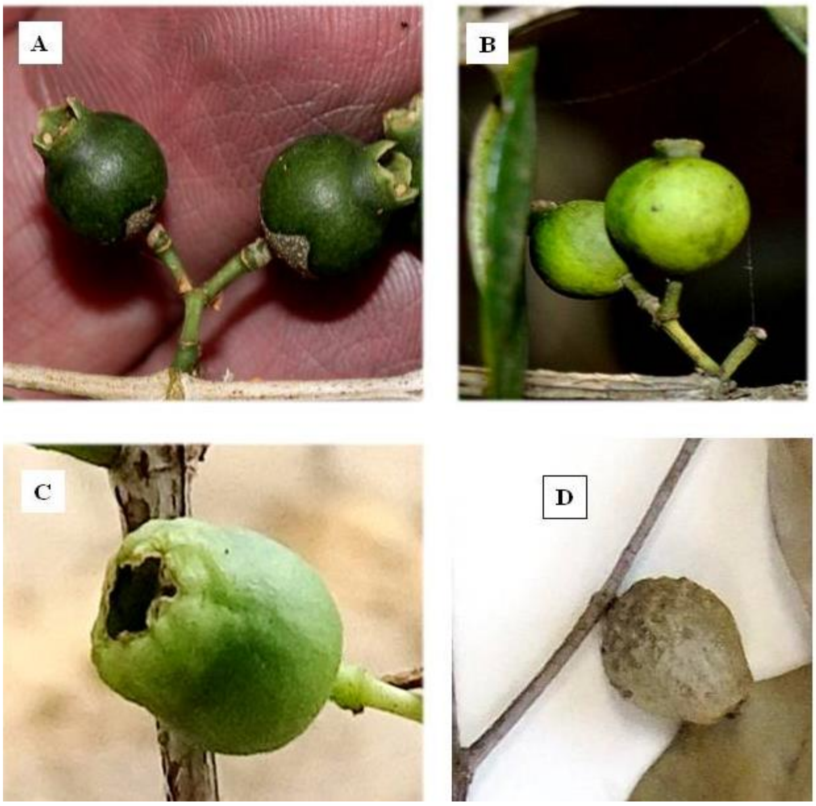


Figure 2.15. Fruits of **A**. *Memecylon* sp. nov. 1 (photo by David Styles). **B**. *M*. sp. nov. 3 (photo by John Burrows). **C.** *M. incisilobum* (photo by Hermenegildo Matimele). **D**. *M. rovumense* (*Clarke 56*, K; photo by Dr R. D. Stone).

2.3.6.2. Fruit size

The fruit varies greatly in size among taxa, ranging mostly between 7–8 × 4–8 mm (*M. natalense*, *M. incisilobum*, *M. nubigenum*, *M. aenigmaticum*, *M.* sp. nov. 1, *M.* sp. nov. 2, *M.* sp. nov. 3). In *M. bachmannii* the fruits are larger 4–10 (–14) × 4–6 (–10) mm. In *M. rovumense* the fruits are relatively large (18 × 14 mm) in comparison to the rest of the taxa.

2.3.6.3. Fruit calycinal crown

The top of the fruit has a persistent calycinal crown 1 to 2 mm high, except in *M. aenigmaticum* where the crown is very short (ca. 0.3 mm). In *M. incisilobum* the calycinal crown is thickened and collar-like with the lobes curved inwards.

2.3.6.4. Fruit surface texture

In most of the studied taxa the surface of the fruit is smooth. Only the fruits of *M. rovumense* and *M. aenigmaticum* are conspicuously verrucose-wrinkled (Fig. 2.16).

In all the studied taxa, the surface of the fruit is smooth. Except the fruits of *M. rovumense* and *M. aenigmaticum* which are conspicuously verrucose-wrinkled (Fig. 2.16).

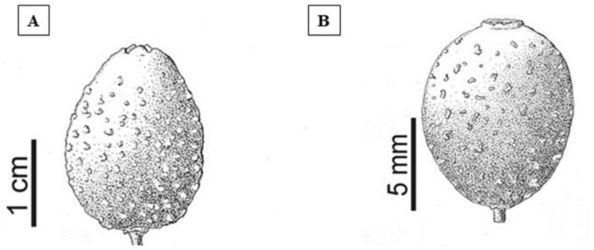


Figure 2.16. Fruits with verrucose-wrinkled surface texture (line drawings reproduced from Stone et al., 2017b). **A**. *Memecylon rovumense* (*Clarke 56*, K). **B**. *M. aenigmaticum* (*Timberlake et al.* 5574, K).

2.4. Conclusion

Classifications based on morphological characters are mostly practical for users who would not be able to identify species based solely on molecular techniques (Dunn, 2003). Morphologically, the *Memecylon natalense* species-complex has diverse diagnostic characters that are useful in delimiting its members. There is high degree of polymorphism in the members of *M. natalense* species-complex, in both the geographically narrowly distributed local endemics (i.e. *M. rovumense*, *M.* sp. nov. 2 and *M.* sp. nov. 3) and more widely distributed taxa (i.e. *M. natalense* and *M. bachmannii*). In other study groups (e.g. figs) polymorphism complicates identification and the situation is further compounded given that these species are already semi-cryptic. This seems to be the case in the *M. natalense* species complex also. Additionally, it should be noted that the Xiao et al. (2010) study was only cited as an example for a situation where polymorphisms and cryptic speciation makes taxonomic identification challenging. Diagnostic characters in the study group include leaves (shape, base, apex, texture and size), petiole length, penduncle length, shape of hypantho-calyx, shape of corolla in bud, petal shape, colour of the anther connectives, and fruits (shape, size, surface texture, calycinal crown). Persistent bracteoles are present in *M. bachmannii* and *M.* sp. nov. 2, setting these two taxa apart from the others in this study. All the taxa show considerable variability in leaf shape, leaf base, and leaf apex.

CHAPTER 3: NUMERICAL TAXONOMY

3.1. Introduction

Memecylon section *Buxifolia* is a monophyletic group with an overall range from East Africa (Kenya and Tanzania) southwards to the eastern part of South Africa, and a disjunct distribution in western and northern Madagascar (Stone, 2014). Until recently, the circumscription of *M*. sect. *Buxifolia* has included fourteen species (Stone, 2014; Stone et al., 2017b). In South Africa there are two species, *M. bachmannii* and *M. natalense* based on recent treatments (e.g. Coates-Palgrave, 2002; Germishuizen et al., 2006; Boon, 2010). These species are quite distinct at the morphological level (Van Wyk, 1983), and their recognition as separate species has never been questioned. Morphologically, *M. natalense* differs from *M. bachmannii* mainly by its smaller, usually petiolate and ovate leaves, acute or cuneate lamina base, long branched peduncles and flowers with deciduous subtending bracts (versus larger, short-petiolate, broadly rounded to rounded leaves, rounded or shallowly cordate lamina base, compressed peduncles and flowers with three pairs of persistent, opposite-decussate bracts) (Van Wyk, 1983).

Molecular evidence suggests that the *M. natalense* species-complex includes several semi-cryptic lineages that are morphologically similar to the SA endemic *M. natalense* (Stone et al., 2017a). In the present study, phenetic (numerical) methods are used to resolve taxonomic uncertainties among members of the *M. natalense* species-complex in southern Africa. Morphological data are analysed, and Operational Taxonomic Units (OTUs) are grouped into clusters based on overall similarity (Sneath and Sokal, 1962). Morphological characters are weighted equally, and similarity alogorithms are employed with the aim of obtaining objective groupings (Sokal and Sneath, 1973).

Numerical taxonomy has long been criticised for being subjective (Blackwelder, 1967; Gower, 1988). Objectivity is lost when the taxonomist decides on the units, features and characters to be taken into account, and also because of the mathematical and statistical choices made during the analysis (Gower, 1988). Furthermore, there are problems with clustering methods (Sneath, 1970; Everitt, 1974), and the choice of methods to be used. There is constant debate between taxonomists and statisticians (Bridge, 1993), as different clustering methods yield different results based on the same set of character data (Sneath, 1970; Marriot, 1971; Everitt, 1974).

Lastly, one of the critical limitations of numerical taxonomy is its non-evolutionary approach (Sneath, 1970). Because variation in individual characters is reduced to a measure of overall similarity, the relationships between individual characters and the resulting phenogram cannot be interpreted. Consequently, the ability to distinguish between homology and analogy (homoplasy) becomes problematic (Sneath, 1970; Everitt, 1974). The purpose of phenetics has never been to determine relationships. In an evolutionary sense, the branches on the phenogram have no meaning. Phenetic groupings are in some cases based on shared ancestral features (symplesiomorphies) or on features shared due to evolutionary convergence. In this way, the phenetic approach can lead to paraphyletic or polyphyletic groupings, in contrast to the criterion of monophyly which Hennig (1966) argued is the only truly objective means of classification. Hence, the groupings found in this study will only reflect overall similarity or dissimilarity among the OTUs, while evolutionary relationships among OTUs will be dealt with in Chapter 4.

However, despite its many drawbacks, numerical taxonomy is a comprehensive method of summarizing data that aims to produce objective groupings (Sokal and Sneath, 1973). Since their introduction by Sneath and Sokal (1962), numerical methods have been widely applied in various systematic studies of plant where classification and delimitation are difficult to achieve using conventional taxonomic methods (Sneath and Sokal, 1973; Sneath, 1995).

The investigated taxa include the two previously recognised South African species *M. natalense* and *M. bachmannii*. Additionally, the present study included several other OTUs:

- A coastal population *M. incisilobum* from southern Mozambique (Gaza province near Praia do Bilene).
- Another coastal population *M.* sp. nov. 1 from northeastern KZN (Kosi Bay Nature Reserve), separated from *M. incisilobum* by an aerial distance of ca. 200 km. These two populations were initially considered to be a single species because of their 100% nrDNA sequence identity (Stone, 2014; Stone et al., 2017a).
- *M. nubigenum* from northern Mozambique and southern Malawi (Mt Mulanje). This species was previously identified as *M. natalense* in the *Flora Zambesiaca* (Fernandes and Fernandes, 1978).

- *M. rovumense* from southern Tanzania (Lindi District).
- *M. aenigmaticum* from northern Mozambique (Cabo Delgado Province).
- *M.* sp. nov. 2, a small-leaved population from the Eastern Cape (Hluleka and Dwesa-Cwebe Nature Reserves) sharing some morphological features with *M. natalense* and others with *M. bachmannii*.
- *M.* sp. nov. 3 from Limpopo province (Soutpansberg).

3.2. Materials and Methods

3.2.1. Specimen selection

Each specimen was treated as an independent OUT following Sokal and Sneath (1962). Only fruiting specimens were used because some OTUs (e.g., *M. aenigmaticum*) did not have flowering material. A total of 61 specimens were examined (Appendix A) consisting of material kept in the Bews (NU) and Ward (UDW) herbaria, additional specimens received on loan from other institutions (BNRH, K, NH, PRE, PRU), and field-collected specimens.

3.2.2. Character selection

A total of 20 vegetative and fruit characters were selected for phenetic analysis. These comprised both quantitative (n= 8) and qualitative (n= 12) characters (Table 3.1). It is important to choose characters that are not affected by environmental conditions (Sneath and Sokal, 1973). Thus, plant characters such as tree height and leaf colour were excluded from the analyses. The character-states were scored as binary or multistate variables. For quantitative (continuous) characters, breaks between groups were determined by a “range scaling procedure” (Thorpe, 1984) in SPSS version 25 (International Business Machines [IBM] Corp., 2017) using a parametric range test (Tukey’s test) in conjunction with One-way ANOVA. Data sets that were not normally distributed or did not have equal within-group variance were log transformed (leaf length, leaf width, acumen length, petiole length, fruit length, fruit width, pedicel length). Characters were excluded from the analysis if the ANOVA results were not statistically significant after being log transformed (e.g. calycinal crown lobes 1–2 [–3] × 1–2 mm). The binary and multistate variables were then used to construct a character-matrix (Appendix B).

Table 3.1. Characters and character-states used in the phenetic analysis.

Characters	Character-states & numeric codes
1. Internode length	1. ≤ 30 mm = 0 2. 31 – 40 mm = 1 3. ≥ 41 mm = 2
2. Leaf shape	4. Elliptic = 0 5. Elliptic ovate = 1 6. Broadly elliptic ovate = 2 7. Broadly ovate = 3 8. Suborbicular = 4 9. Ovate = 5 10. Obovate = 6
3. Leaf texture thickly coriaceous	11. [0= absent/ 1= present]
4. Leaf length	12. ≤ 54 mm = 0 13. 55 – 59 mm = 1 14. ≥ 60 mm = 2
5. Leaf width	15. ≤ 36 mm = 0 16. 37 – 47 mm = 1 17. ≥ 48 mm = 2
6. Leaf apex shape	18. Acuminate = 0 19. Obtusely acuminate = 1 20. Rounded = 2 21. Acute = 3 22. Obtuse = 4
7. Acumen length	23. ≤ 2 mm = 0 24. 3 – 5 mm = 1 25. 6 – 8 mm = 2
8. Base width	26. ≤ 25 mm = 0 27. 26 – 38 mm = 1 28. 39 – 54 mm = 2 29. ≥ 55 mm = 3

9. Fruit shape	30. Broadly pyriform = 0 31. Subglobose = 1 32. Ellipsoid = 2 33. Obovoid = 3
10. Fruit length	34. ≤ 4 mm = 0 35. 5 – 8 mm = 1 36. 9 – 14 mm = 2
11. Fruit width	37. 4 mm = 0 38. 5 – 11 mm = 1 39. 12 – 14 mm = 2
12. Fruit pedicel length	40. 2 mm = 0 41. 3 – 5 mm = 1 42. 6 – 8 mm = 2 43. 9 – 14 mm = 3
13. Fruit calycinal lobes with scarious teeth	44. [0= absent/ 1= present]
14. Fruit calycinal lobes curvature	45. [0= absent/ 1= present]
15. Fruit calycinal lobe apex	46. Subacute = 0/ Rounded = 1
16. Fruit calycinal lobe shape broadly deltate	47. [0= absent/ present= 1]
17. Fruit bracteoles	48. [Persistent= 1/ Deciduous= 0]
18. Fruit wrinkles	49. [0= absent/ 1= present]
19. Fruit lobes arrangement	50. Lobes partially concealing to epigynous chamber = 1/ Fruit lobes radially partitioned = 0
20. Fruit calycinal crown thickness	51. [0= absent/ 1= present]

3.2.3. Statistical analysis

The phenogram was generated using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) (Sokal and Michener, 1958), with the *hclust* function (https://stat.ethz.ch/R-manual/R-devel/library/stats/html/hclust.html), using the hierarchical clustering method “Euclidian” in R software (R Core Team, 2017).

3.3. Results

The UPGMA phenogram is shown in Figure 3.1. There are two main clusters (denoted by the letters A and B). Cluster A consists of *M. bachmannii* specimens (*n*= 15). Cluster B consists of six subclusters: B1 is composed of *M. incisilobum* (*n*= 1); B2 includes specimens of *M.* sp. nov. 1 (*n*= 2); B3 is composed of *M. aenigmaticum* (*n*= 1); B4 represents *M. rovumense* (*n*= 1); and B5 is composed of *M. nubigenum* specimens (*n*=6). Subcluster B6 is composed of specimens of *M. natalense*, *M.* sp. nov. 2 and *M.* sp. nov. 3 (*n*= 25). The numerical principals followed in this study follows that of Sneath and Sokal (1973) in which they reported that “when a hierarchical tree has been made, the line defining a given rank must be a straight line drawn across it at some affinity level. The line must not bend down according to personal and preconceived whims about the rank of the taxa”. The distance where phenon lines are drawn is subjective (Everitt, 1974), and more often they correspond with recognized taxa. The issue of comparing phenetics and cladistics results is dealt with below.

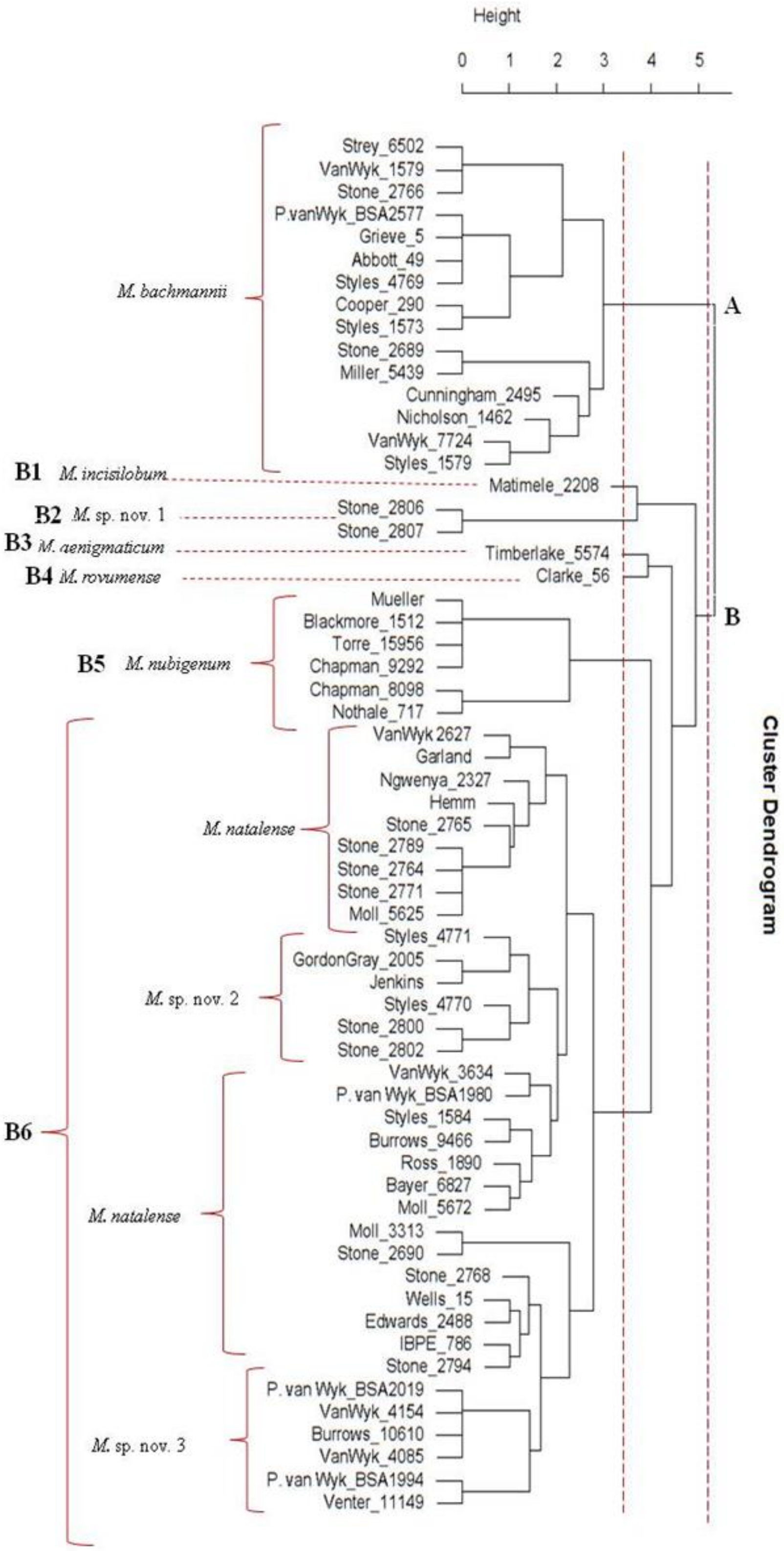


Figure 3.1. UPGMA phenogram of *Memecylon* fruiting specimens. Two discrete clusters (A and B) are delineated with a phenon line drawn at a distance of 5. Within cluster B, there are six discrete subclusters (phenon line at a distance of 3.5).

Another clustering method was also performed (Neighbour-Joining [Saitou and Nei, 1987]), the results of which did not correspond well to the taxa recognized (data not shown).

3.4. Discussion

Memecylon bachmannii specimens are exclusively found in UPGMA cluster A (Fig. 3.1, A). In comparison to other *Memecylon* taxa investigated, this species has much larger, broadly ovate to suborbicular leaves 40–90 (–100) × 30–50 (–65) mm, larger persistent opposite-decussate bracteoles (versus smaller persistent opposite-decussate bracteoles in *M*. sp. nov. 2), and much shorter petiole, pedicel and peduncles, usually 0.5–2 mm (versus slightly longer petiole, pedicel and peduncles ranging from 1–5 mm in *M. natalense*). The phenetic results indicate that this taxon is morphologically distinct in comparison to the other taxa in this study.

Memecylon incisilobum (Fig. 3.1, subcluster B1) and *M.* sp. nov. 1 (Fig. 3.1, subcluster B2) they cluster with one another indicating that these two taxa are more similar to each other than to the other species found in cluster B. These two populations were previously found to have 100% nrDNA sequence identity (Stone et al., 2017a), but there are several morphological differences between them (Stone et al., 2017b). *Memecylon incisilobum* is clearly distinguished from *M.* sp. nov. 1 by its fruits with calycinal crown thickened (versus calycinal crown not thickened) and calyx-lobes that are curved inwards (versus erect lobes that are acute in shape).

Memecylon incisilobum is also distinguished from *M. natalense* by its broadly and obtusely acuminate leaf apex (versus acuminate to acute leaf apex); fruits with calycinal crown that are thickened and collar-like with inwardly curved lobes (versus fruit calycinal crown that are not thickened or collar-like and not curved inward), and calyx-lobes with scarious margin (versus margin not scarious). *Memecylon* sp. nov. 1 differs from *M. natalense* in having elliptic to obovate leaf-blades that are broadly and obtusely acuminate at the apex (versus leaf-blades elliptic to broadly elliptic-ovate with apex acuminate to acute); and fruits with calyx-lobes rounded and scarious (versus calyx-lobes acute, margin not scarious).

The specimen *Clarke 56* representing *M. rovumense* (Fig. 3.1, subcluster B4) grouped closely with *M. aenigmaticum* (Fig. 3.1, subcluster B3), in agreement with Stone et al. (2017b) who concluded that these two taxa appear closely related. *Memecylon aenigmaticum* differs from *M. rovumense* by its much smaller leaves 17.5–30 × 10–17.5 mm (versus larger leaves 33–55 × 17–33 mm) and smaller ellipsoid to obovoid fruits 9–10.5 × 7–8 mm (versus larger, ovoid to broadly pyriform fruits 18 × 14 mm).

Memecylon rovumense has been previously confused with *M. natalense*, but nrDNA evidence suggests it may have originated through hybridization between a lineage close to the Kenyan *M. fragrans* A. Fernandes & R. Fernandes and another, as-yet unidentified Mozambican lineage close to *M. torrei* A. Fernandes & R. Fernandes (Stone et al. 2017a). At the morphological level, *M. rovumense* differs from *M. natalense* by its more thickly coriaceous leaves with rounded to obtuse apex (versus thinly coriaceous leaves with apex acute to acuminate); and larger, conspicuously verrucose-wrinkled fruits 18 × 14 mm, lacking a persistent calycinal crown but with broadly deltate, inward-curving lobes (versus smaller fruits up to 10 mm in diameter, with a smooth exterior and persistent calycinal crown having erect, acute lobes).

Memecylon aenigmaticum has also been confused with the South African *M. natalense* but differs by its thickly coriaceous, obovate leaves (versus leaves thinly coriaceous and broadly elliptic-ovate); and obovoid, verrucose-wrinkled fruit (versus smooth and ellipsoid to subglobose fruit). The phenetic results (Fig. 3.1) clarify that *M. aenigmaticum* and *M. rovumense* are morphologically similar to each other, and different from *M. natalense.*

Fernandes and Fernandes (1978) expanded the circumscription of *M. natalense* to include collections from northern Mozambique and southern Malawi (Mt Mulanje). Recently, however, the Mulanje population has been shown to be quite distinct from *M. natalense* at the molecular level (Stone et al., 2017a), and these montane populations were described as a separate species, *M. nubigenum* (Stone et al., 2017b). This taxon has obtuse apex (versus acuminate to acute leaf apex in *M. natalense*) and subglobose fruits 7(–8) mm in diameter (versus ellipsoid fruit 8–10 mm diameter). In the phenogram (Fig. 3.1, subcluster B5), *M. nubigenum* grouped separately from *M. natalense sensu stricto*. These morphological results confirm that *M. nubigenum* is indeed different from *M. natalense*.

The small-leaved *Memecylon* from Hluleka and Dwesa-Cwebe Nature Reserves (herein referred to as *M.* sp. nov. 2) grouped with two groups of *M. natalense* (Fig. 3.1, subcluster B6). In a previous nrDNA study these populations were named *M.* aff. *bachmannii* (Stone et al., 2017a), due to the presence of ovoid fruit that is closely subtended by three pairs of persistent, opposite-decussate bracteoles that also occur in *M. bachmannii,* in contrast to *M. natalense* where there are ellipsoid to subglobose fruits and rapidly deciduous bracteoles. Some specimens from Dwesa-Cwebe Nature Reserve (*Gordon-Gray 2005*, NU; *Styles 4770*, NU; *Styles 4771*, NU) also have leaf shapes similar to those of *M. bachmannii* (broadly ovate to suborbicular leaf blades, rounded to shallowly cordate leaf bases and abruptly acuminate leaf apices). On the other hand, the fruit size of *M*. sp. nov. 2 is 4–7 × 3–5 mm, much smaller in comparison to the fruits of *M. bachmannii* with dimensions of 5–9 (–15) × 4–10 (–12) mm. The leaf size of *M*. sp. nov. 2, with dimensions (40–) 46 × 25 (–34) mm, is similar to that of *M. natalense* but unusually small in comparison to *M. bachmannii* with leaf dimensions of (40–) 90 × 30–50 (–70) mm. Moreover, the leaf shape in some specimens of *M*. sp. nov. 2 (*Jenkins s.n*. PRE; *Stone et al. 2800*, NU; *Stone et al. 2802*, NU) is more similar to *M. natalense* in being broadly ovate to broadly elliptic-ovate, with cuneate base and acute apex. Despite the fact that *M*. sp. nov. 2 shares certain character-states with *M. bachmannii*, the phenetic results indicate that it has greater overall similarity with *M. natalense*.

Additionally, *M*. sp. nov. 3 also grouped with *M. natalense* (Fig. 3.1, subcluster B6), but made a distinct subcluster within this group. This taxon has ovate leaf-blades with an obtuse or nearly rounded base (versus broadly elliptic ovate and cuneate leaf base). The fruits resemble those of *M. natalense* in being ellipsoid to subglobose, 7–10 mm in diameter, with persistent calycinal crown and erect acute lobes about 1 mm high. Despite the distinctive leaf characters and petiole length, the phenetic results indicate that *M*. sp. nov. 3 has overall similarity to both *M. natalense* and *M*. sp. nov. 2.

CHAPTER 4: CLADISTICS

4.1. Introduction

Memecylon section *Buxifolia* currently comprises 14 species and has an overall range from Kenya and Tanzania southward to eastern South Africa (Stone, 2014; Stone et al., 2017b). Monophyly of this section was well-supported in previous studies based on phylogenetic analysis of nuclear rDNA spacer sequences and extensive sampling of *Memecylon* in tropical Africa and Madagascar (Stone, 2014; Stone et al., 2017a). However, *M. natalense sensu lato* was not monophyletic (was paraphyletic) and included some geographically outlying populations (in Malawi, Tanzania, Mozambique and South Africa) representing distinct evolutionary lineages. Moreover, South African *M. natalense sensu stricto* was also not exclusively monophyletic and, surprisingly, was found to have 100% sequence identity or nearly so with the morphologically distinct *M. bachmannii*. In this chapter, I present the results of a cladistic analysis of morphological characters that aims to reconstruct phylogenetic relationships amongst members of the *M. natalense* species-complex. Another aim of this investigation was to compare the results of the morphological cladistic analysis with phenetic (Chapter 3) and earlier molecular phylogenetic results (Stone, 2014; Stone et al., 2017a, see Fig. 4.2.).

Cladistics originated with the studies of the German entomologist Willi Hennig, who sought to establish a truly historical approach to systematics that provides an understanding of evolutionary relationships of various organisms (Hennig, 1966). This was also an attempt to overcome problems associated with subjective methods by developing an approach that could clearly infer phylogenetic relationships (Williams and Ebach, 2007). Moreover, cladistics together with numerical taxonomy were both borne out of a desire for greater objectivity and for classification based on comprehensive analysis of characters, rather than "cherry picking" characters believed *a priori* to have evolutionary importance as observed in evolutionary taxonomy (Hull, 1990). Homology is an important concept for fully comprehending the principles and methodology of cladistics (Patterson, 1982; Hillis et al., 1994). Synapomorphies are homologous structures whose traits are shared by related taxa, thus revealing their common ancestry (Hennig, 1966). Therefore, the goal of cladistics can be summarized as a method that produces testable hypotheses of genealogical relationships among organisms, based on synapomorphies which pass from recent common ancestors through genealogical descent (Scott-Ram, 1990).

Maximum Parsimony is the tree-building method used in the present study. In this method, multiple trees are evaluated, and the best hypothetical phylogeny is the one that requires the smallest number of character-state changes across all characters. In this way, character congruence (homology) is maximised, and character conflict (homoplasy) is minimised (Patterson, 1988). The "most parsimonious tree" is one that requires the fewest character changes (Camin and Sokal, 1965; Bonde, 1977; Sober, 1983).

The investigated taxa included the previously recognized South African species *M. natalense* and *M. bachmannii* as well as several other OTUs:

I. *M. incisilobum* from southern Mozambique (Gaza Province)
II. *M. nubigenum* from mountains of northern Mozambique and southern Malawi
III. *M. rovumense* from coastal forests in southern Tanzania (Lindi Region) and northern Mozambique (Cabo Delgado)
IV. *M. aenigmaticum* from northern Mozambique (Cabo Delgado Province)
V. *M.* sp. nov. 1, a coastal population from northeastern KwaZulu-Natal (near Kosi Bay)
VI. *M.* sp. nov. 2, a small-leaved population from the Hluleka and Dwesa-Cwebe nature reserves (Eastern Cape)
VII. *M.* sp. nov. 3 from Limpopo Province (Soutpansberg).

4.2. Materials and methods

4.2.1. Ingroup

The examined material (61 specimens representing the ingroup) were available as specimens kept in the Bews (NU) and Ward (UDW) herbaria or received on loan from other institutions (see Appendix C). Only fruiting specimens were used because some OTUs (e.g., *M. aenigmaticum*) did not have flowering material.

4.2.2. Outgroup species selection

Evolutionary polarity of characters can be traced using the method of outgroup comparison (Bryant, 2001). In the present study, the East African species *M. cogniauxii* Gilg and *M. deminutum* Brenan were selected for the outgroup, on the basis that they belong to the larger, predominantly East African clade in which sect. *Buxifolia* is phylogenetically nested (Stone, 2014). Some characters (e.g. anther gland) information for these outgroup species were obtained from literature sources (Stone, 2014), not from herbarium or living material.

4.2.3. Morphological characters and character analysis

A total of 22 vegetative and fruit characters was selected for cladistics analysis. These comprised both quantitative (*n*= 8) and qualitative (*n*= 14) characters (Table 4.1). The character-states were scored as binary or multistate variables. For quantitative (continuous) characters, breaks between groups were determined by a "range scaling procedure" (Thorpe, 1984) in SPSS version 25 (International Business Machines [IBM] Corp., 2017) using a parametric range test (Tukey's test) in conjunction with One-way ANOVA. Data sets that were not normally distributed or did not have equal within-group variance were log transformed (leaf length, leaf width, acumen length, petiole length, fruit length, fruit width, pedicel length). Characters were excluded from the analysis if the ANOVA results were not statistically significant after being log transformed (e.g. calycinal crown lobes 1–2 [–3] × 1–2 mm). The binary and multistate variables were then used to construct a character-matrix (Appendix D). Uninformative characters were excluded, and missing data (0.3%) were treated as uncertainty.

Table 4.1. Characters and character-states used in the cladistic analysis.

	Characters		**Character States and codes**
1.	Internode length	1.	≤ 30 mm = 0
		2.	31 – 40 mm = 1
		3.	≥ 41 mm = 2
2.	Leaf shape	4.	Elliptic = 0
		5.	Elliptic ovate = 1
		6.	Broadly elliptic ovate = 2
		7.	Broadly ovate = 3
		8.	Suborbicular = 4
		9.	Ovate = 5
		10.	Obovate = 6
3.	Leaf texture thickly coriaceous	11.	[0= absent/ 1= present]

4. Leaf length	12. ≤ 54 mm = 0 13. 55 – 59 mm = 1 14. ≥ 60 mm = 2
5. Leaf width	15. ≤ 36 mm = 0 16. 37 – 47 mm = 1 17. ≥ 48 mm = 2
6. Leaf apex shape	18. Acuminate = 0 19. Obtusely acuminate = 1 20. Rounded = 2 21. Acute = 3 22. Obtuse = 4
7. Acumen length	23. ≤ 2 mm = 0 24. 3 – 5 mm = 1 25. 6 – 8 mm = 2
8. Base width	26. ≤ 25 mm = 0 27. 26 – 38 mm = 1 28. 39 – 54 mm = 2 29. ≥ 55 mm = 3
9. Fruit shape	30. Broadly pyriform = 0 31. Subglobose = 1 32. Ellipsoid = 2 33. Obovoid = 3
10. Fruit length	34. ≤ 4 mm = 0 35. 5 – 8 mm = 1 36. 9 – 14 mm = 2
11. Fruit width	37. 4 mm = 0 38. 5 – 11 mm = 1 39. 12 – 14 mm = 2
12. Fruit pedicel length	40. 2 mm = 0 41. 3 – 5 mm = 1 42. 6 – 8 mm = 2 43. 9 – 14 mm = 3

13. Fruit calycinal lobes with scarious teeth	44. [0= absent/ 1= present]
14. Fruit calycinal lobes curvature	45. [0= absent/ 1= present]
15. Fruit calycinal lobe apex	46. Subacute = 0/ Rounded = 1
16. Fruit calycinal lobe shape broadly deltate	47. [0= absent/ present= 1]
17. Fruit bracteoles	48. [Persistent= 1/ deciduous= 0]
18. Fruit wrinkles	49. [0= absent/ 1= present]
19. Fruit lobes arrangement	50. Lobes partially concealing to epigynous chamber = 1/ Fruit lobes radially partitioned = 0
20. Fruit calycinal crown thickness	51. [0= absent/ 1= present]
21. Aphyllous nodes	52. [0= absent/ 1= present]
22. Anther connective	53. [0= absent/ 1= present]

4.2.4. Data analysis

The character matrix was analysed using equally weighted, unordered parsimony (Fitch, 1971) implemented in the software package PAUP*, version 4.0 beta 10 (Swofford, 2002). A thorough heuristic search of the data set was found to be impractical. Instead, searches of “tree space” were performed with an accelerated search strategy known as the parsimony ratchet (Nixon, 1999), implemented using PAUPRat version 1 beta (Sikes and Lewis, 2001). The ratcheting strategy relies on iterative perturbations of the “tree landscape” in order to escape from local optima much faster. For the current analysis, 100 separate ratchet-aided searches were completed, each with 200 iterations per search. In each iteration, three randomly selected characters were initially upweighted, and one tree was saved. Of the 20,100 trees in the combined tree file there were 19,669 most-parsimonious trees (length=88 steps) found using the “filter” command in PAUP*.

The consensus of minimum-length trees obtained using the parsimony ratchet is expected to be the same as that from conversional heuristic search, assuming that the number of ratchet searches performed has been sufficient (Nixon, 1999). The amount of homoplasy in the data set was evaluated using the consistency index (Kluge and Farris, 1969) and the retention index (Farris, 1989).

4.3. Results

The majority-rule consensus tree is shown in Figure 4.1. The numeric values shown on the branches are proportion of trees having that branch amongst the collection of 19,669 most-parsimonious trees. Appendix E gives details of the characters (synapomorphies) supporting clades, as well as the consistency index (CI) values indicating the robustness of these synapomorphies.

The ingroup samples Clade A (representing *M.* sect. *Buxifolia*) are a monophyletic group, appearing in 100% of the most-parsimonious trees. There are three distinct clades delimited: Clade B consists of *M. rovumense* + *M. aenigmaticum*, Clade C consists of *M. bachmannii*, Clade D consists of *M. incisilobum* + *M.* sp. nov. 1. and Clade E consists of *M. nubigenum*. The terminals representing *M. natalense*, *M.* sp. nov. 2 and *M.* sp. nov. 3 samples, appear in an unresolved polytomy. Clade F and G consist of *M.* sp. nov. 3.

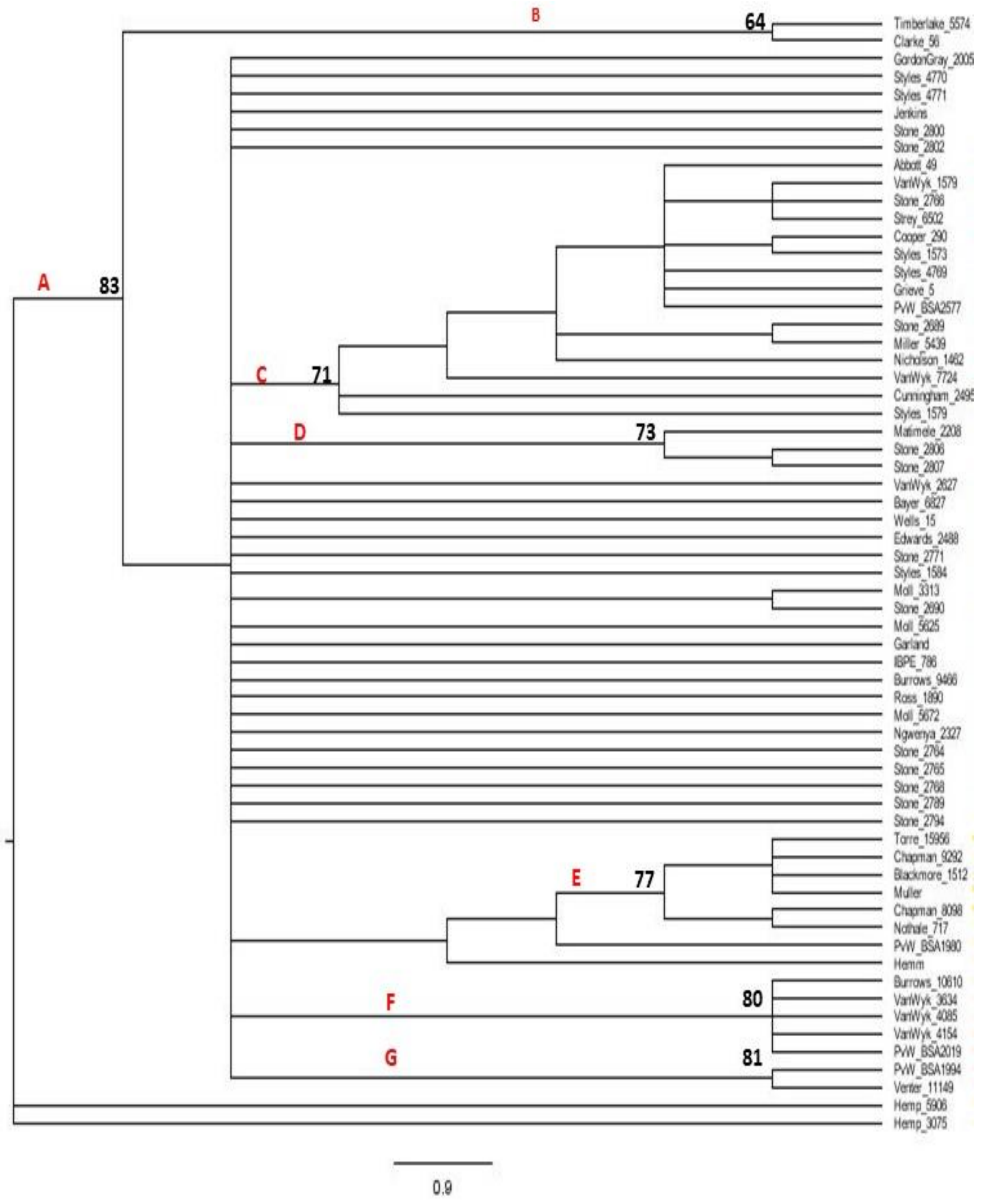


Figure 4.1. Majority-rule consensus of 19,669 most-parsimonious trees (length=88 steps). Numeric values shown on the branches are the proportion of MPTs having that branch (not bootstrap values). The OTUs are represented by colour codes: *Memecylon natalense* – green; *M. bachmannii* – blue; *M. incisilobum* – brown; *M. nubigenum* – yellow; *M. rovumense* – grey; *M. aenigmaticum* – purple; *M.* sp. nov. 1 – pink; *M.* sp.

nov. 2 – black; *M.* sp. nov. 3 – red; outgroups – orange. Alphabets represent clades (see results for details).

4.4. Discussion

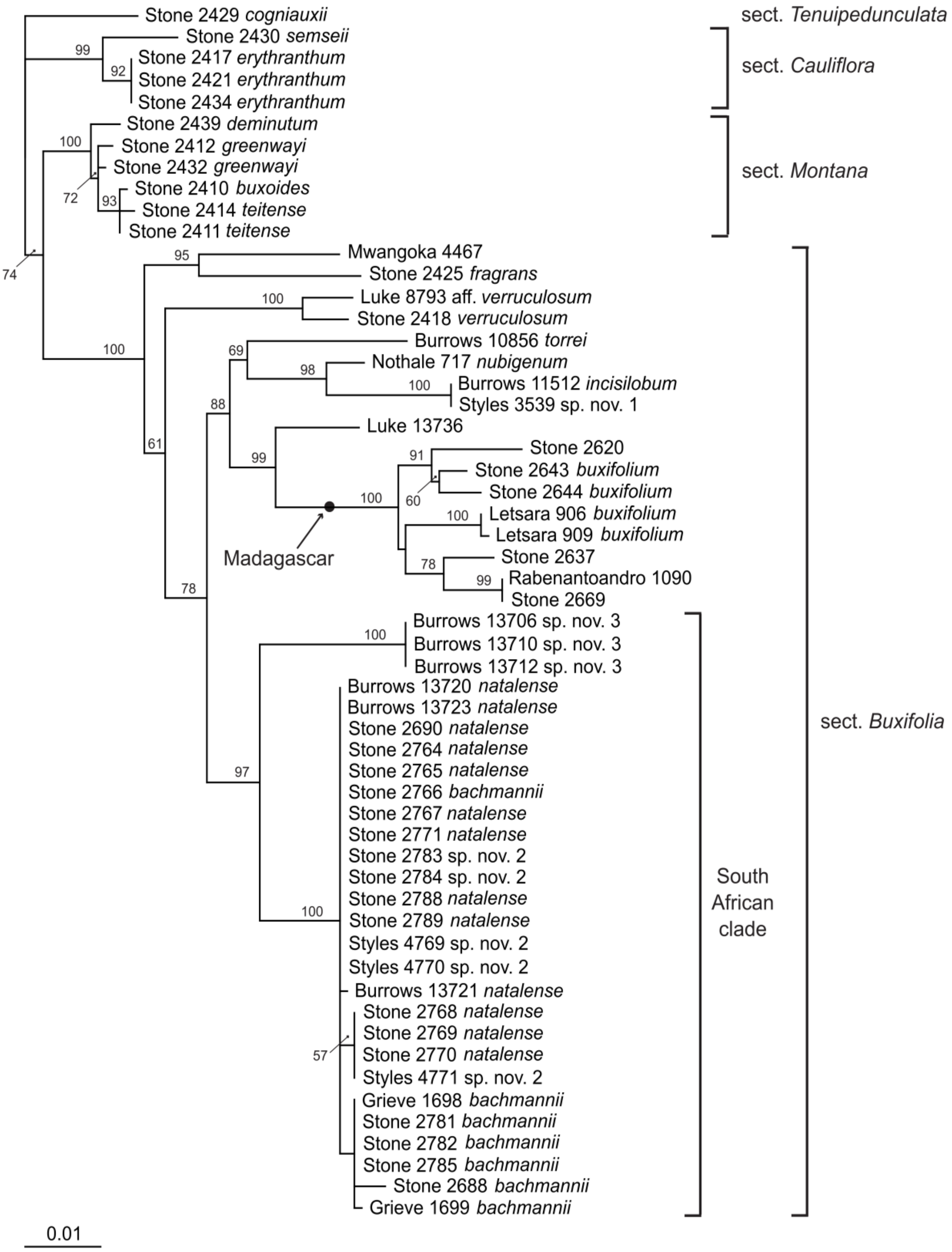


Figure 4.2. Outgroup-rooted maximum likelihood tree from combined analysis of ITS1, ITS2 and 5′ ETS sequences (reproduced from Stone et al., 2017a). Branch lengths are

drawn proportionally to the estimated amount of change; the scale bar at lower left is in units of mean number of substitutions per site. Bootstrap proportions are shown above branches (values <50% not shown).

The results of the cladistic analysis were compared with the previous molecular study by Stone (2014) and Stone et al. (2017a). Comparison was also made with the phenetic results in Chapter 3. The underlying philosophy, reasoning and methodology of the phenetic and cladistic analyses are vastly different (discussed in in Chapter 3).

Samples of *M.* sect. *Buxifolia* are monophyletic in the present study represented in Fig. 4.1 by clade A with a proportion number of 83. This is in agreement with the previous molecular results shown in Fig. 4.2. Sect. *Buxifolia* is supported by three robust synapomorphies (namely: Character 11 - fruit width; Character 20 - aphyllous nodes; Character 21 - anther connective gland present) with CI value of 1.000 indicating no homoplasy. Additionally, there is moderate homoplasy (CI = 0.600) in Character 2 (leaf shape) for this node (Appendix E).

Memecylon rovumense + *M. aenigmaticum* samples formed clade B, in agreement with the results of the phenetic analysis (Chapter 3), These taxa share a locality in Cabo Delgado province in northern Mozambique (Stone et al., 2017b). Neither *M. aenigmaticum* nor *M. rovumense* were sampled in the combined analysis of ITS1, ITS2 and 5′ ETS sequences (Fig. 4.2), but *M. rovumense* was sampled in another ITS1+ITS2 analysis (see Fig. 1 in Stone et al., 2017a). In the ITS analysis, *M. rovumense* and *M. fragrans* were in a strongly supported clade (BP = 97% and 99%). However, in the ETS analysis *M. rovumense* belonged to a different group that also included sequences of the Mozambican species *M. torrei*. This lineage was moderately supported (BP 67%). At the morphological level, *M. rovumense* was closely allied with *M. natalense* (Stone et al., 2017a). The leaves, however, appear more-or-less intermediate between *M. fragrans* and *M. torrei* suggesting that it is possibly a homoploid hybrid species (Stone et al., 2017a). Clade B with a proportion number of 64 is supported by Character 10 - fruit length and Character 18 - fruit with verrucose wrinkles (both with CI= 1.000). Moderate homoplasy was seen in Character 2 (leaf shape obovate with CI= 0.600), and high homoplasy in Character 9 (fruit shape broadly pyriform in *M. rovumense* and elliptic to obovoid in *M. aenigmaticum* with CI= 0.250) and Character 16 (fruit lobe apex with CI= 0.273) (Appendix E).

Memecylon bachmannii samples formed a monophyletic group represented by Clade C, with a proportion number of 71. These results are entirely congruent with the phenetic results (Chapter 3). Contrary to the molecular results (Fig. 4.2) where *M. natalense*, *M. bachmannii*, *M.* sp. nov. 2 and *M.* sp. nov. 3 together formed a well-supported monophyletic group, the cladistic results suggest that the relationship of *M. bachmannii* to *M. natalense, M.* sp. nov. 1, *M.* sp. nov. 2 and *M.* sp. nov. 3 is equivocal. Despite forming a monophyletic clade, most characters that define Clade C displayed high levels of homoplasy (Character 2 - leaf shape suborbicular, Character 5 - Leaf width, Character 6 - Apex shape, all with CI= 0.600; Character 7 - Acumen length had CI= 0.125; Character 16 - fruit calycinal broadly subacute lobe shape had CI= 0.273; Character 17 - persistent fruit bracteoles had CI= 0.125).

Memecylon incisilobum + *M.* sp. nov. 1 formed Clade D with a proportion number of 73, and their sister relationship is moderately supported by Character - 2 leaf shape, Character 5 - leaf width and character 6 - leaf apex shape with CI= 0.600. Additionally, three characters showed high homoplasy Character 1 - internode length with CI= 0.083, Character 12 - pedicel length with CI= 0.214, Character 13 - fruit calycinal crown scarious teethed on margin with CI= 0.333. Expectedly, the cladistic results corroborate the earlier molecular findings that *M. incisilobum* and *M.* sp. nov. 1 are a monophyletic group with 100% bootstrap support (Stone et al., 2017a). The cladistic results also agree with the phenetic analysis (Chapter 3) where *M. incisilobum* and *M.* sp. nov. 1 OTUs clustered closely together.

Memecylon nubigenum samples formed Clade E with a proportion number of 77. This is in accord with the phenetic results (Chapter 3) where *M. nubigenum* clustered separately from *M. natalense*. Clade E was supported by a robust synapomorphy Character 19 - epigynous chamber lacking radial partitions with CI= 1.000 indicating no homoplasy for this character. High homoplasy was seen for Character 14 (fruit calycinal crown curved inward [CI= 0.333]) and Character 16 (fruit calycinal crown lobe entire [CI= 0.273]).

Memecylon natalense and *M.* sp. nov. 2 formed an unresolved polytomy, while *M.* sp. nov. 3 failed to form a specific monophyletic clade (Clade F and Clade G). In the earlier molecular results (Fig. 4.2), *Memecylon* sp. nov. 3 formed a strongly supported clade that was sister to the unresolved polytomy of *M. natalense*, *M. bachmannii* and *M.* sp. nov. 2. Morphologically the Soutpansberg population appears to have a close affinity to *M. natalense sensu stricto* (pers. obs.). In the phenetic analysis (Chapter 3), *Memecylon natalense*, *M.* sp. nov. 2 and *M.* sp. nov. 3 did not form distinct clusters but grouped together indicating that they are more similar to each other morphologically. *Memecylon* sp. nov. 3 samples failed to form a specific monophyletic clade in this cladistic analysis. In the molecular analysis (Stone et al., 2017a), the samples of *M.* sp. nov. 3 made up a strongly supported South African clade together with those of *M. natalense*, *M. bachmannii* and *M.* sp. nov. 2. These results are somewhat contrary to the phenetic analysis, where *M.* sp. nov. 3 clustered with *M. natalense* and *M.* sp. nov. 2, and *M. bachmannii* grouped independently.

Memecylon sp. nov. 2 combines morphological characters of both *M. natalense* and *M. bachmannii*, but is geographically isolated from both these species. Field collection records shows that *M. bachmannii* occurs only in the coastal regions of southern KwaZulu-Natal and the adjacent Eastern Cape (i.e. Ntsubane near Lusikisiki district, Port St. Johns, Mkambati, Madadana). *Memecylon natalense* occurs in the Eastern Cape only at Lupatana River, Mpahlane River and the Ntsubane-Mbotyi forest complex. These forests are geographically separated from the Hluleka Nature Reserve population, and there are no known localities where the two species occur together. This geographic separation suggests that *M.* sp. nov. 2 is not a product of hybridisation between *M. natalense* and *M. bachmannii* but rather a distinct taxon that may have recently diverged from *M. bachmannii*. *Memecylon rovumense*, is however, a hypothesized homoploid hybrid between *M. fragrans* and *M. torrei* as already discussed (Stone et al., 2017a).

There is an ongoing controversy in plant systematics as to whether molecular or morphological data are better sources of phylogenetic information (Bateman et al., 2006). Most systematic journals currently advocate and encourage phylogenetic investigations based on the combination of molecular and morphological data (Bremer, 1996). DNA barcoding has proven instrumental in detecting species complexes or cryptic species that are morphologically similar and are of importance to conservation biology (Bickford et al., 2007; Neigel et al., 2007; Lahaye et al., 2008; McBride et al., 2009).

Memecylon natalense and *M. bachmannii* are morpho-species that are clearly distinct from each other (Van Wyk, 1983) and their recognition as distinct species has never been questioned (Coates-Palgrave, 2002; Boon, 2010). The minimal interspecific variation observed at the rDNA sequence level suggests that they have recently diverged, in which case there has simply not been enough time for mutations to accumulate at the loci (Stone et al., 2017a). Recently diverged species have acquired only few genetic differences meaning that there are few characters to discriminate them, hence even some morphologically well-differentiated species may share identical DNA sequences, preventing accurate identification (Lou and Golding, 2010). As promising as DNA barcoding is, its use for identification of recently diverged species has been reported problematic in some cases (Meyer and Paulay, 2005; Dexter et al., 2010; Lou and Golding, 2010). The failure of DNA barcodes to properly resolve recently-diverged species can be attributed to population genetic factors of the species involved (Meyer and Paulay, 2005). Another indication that may explain the incongruence between the molecular data and morphology-based taxonomies is rapid radiation (Richardson et al., 2001; Li et al., 2016), which could result in low sequence divergence (Baldwin and Sanderson, 1998; Richardson et al., 2001; Ramdhani et al., 2009; Ragsdale and Baldwin, 2010).

4.6. Conclusion

The morphological cladistic results were congruent with the previous molecular analysis. These results were unexpected, as they did not reflect species-specific lineages that should ideally be monophyletic. This could be for a number of reasons. The character states could have been coded incorrectly, and in such case a different coding method may have yielded different results. Character polarization and transformation needs a more in depth examination with robust outgroup comparisons. The outgroup selection could possibly result in better rooting. There are possibly too few morphological synampomorphies examined to resolve the polytomies. Some synapomorphic characters may not have been captured in this analysis, as only fruiting characters were used and floral characters were excluded. It is unfortunate that a large number of herbarium specimens lacked flowering material (especially of *M. rovumense* and *M. aenigmaticum*). The apparent rarity of flowering events is one of the factors making *Memecylon* a difficult genus to study.

CHAPTER 5: REVISED TREATMENT OF MOZAMBICAN *MEMECYLON* (MELASTOMATACEAE–OLISBEOIDEAE)

5.1 Introduction

Memecylon Linnaeus (1753) is a paleotropical genus of forest shrubs and small trees with 350+ species (Renner et al., 2007 onwards). In accordance with recent morphological evidence and molecular findings (Jacques-Félix 1978a; Bremer, 1982; Stone 2006, 2014; Stone and Andreasen, 2010), it is now circumscribed to exclude the monospecific western and central African genus *Spathandra* Guill. & Perr. (Guillemin et al., 1833), the paleotropical *Lijndenia* Zoll. & Moritzi (in Moritzi, 1846) and the African-Madagascan *Warneckea* Gilg (Gilg, 1904).

The treatment of *Memecylon sensu lato* for the *Flora de Moçambique* (Fernandes and Fernandes, 1980) included six species, of which three have distinctly trinervate to multinervate leaves and are properly placed in *Warneckea*, as *W. sansibarica* (Taub.) (Jacques-Félix, 1978a), *W. sessilicarpa* (A. Fern. & R. Fern.) (Jacques-Félix, 1978a) and *W. sousae* (A. Fern. & R. Fern.) (Coates-Palgrave, 2002). A revised key to the Mozambican species of *Warneckea* is given in Stone and Tenza (2017). The remaining three species have apparently uninervate leaves and belong to *Memecylon sensu stricto*: *M. natalense* Markgr. (Mildbraed, 1934), *M. torrei* A. Fernandes & R. Fernandes (Fernandes and Fernandes, 1972) and *M. insulare* A. Fernandes & R. Fernandes (Fernandes and Fernandes, 1972). These three species were recently placed in *M.* sect. *Buxifolia* R.D. Stone (2014).

Memecylon sect. *Buxifolia* is a monophyletic group with an overall range from East Africa (Kenya and Tanzania) southwards to the eastern part of South Africa and disjunctly in western and northern Madagascar (Stone, 2014). It is diagnosed by the combination of branchlets with successive nodes alternating between normal leaves and reduced, often inflorescence-bearing bracts, white petals with corolla rounded to apiculate in bud, and anther connectives bearing a dorsal oil-gland. Amongst the other sections of East African *Memecylon*, an anther gland is found only in the Tanzanian *M.* sect. *Magnifoliata* R.D. Stone (Stone, 2014), which differs in its cauliflorous habit and ellipsoid to obovoid fruits, while *M.* sect. *Obtusifolia* Engler (Engler, 1921), is characterized by its unusually thick bark, yellowish green leaves and subdeltate-acuminate petals. Section *Obtusifolia* has just one species, *M. flavovirens* Baker (Baker et al. 1897), widely distributed in seasonally dry “miombo” woodlands from Angola through Zambia, Katanga (D. R. Congo), Burundi and Malawi to southwestern Tanzania. In addition, *M. flavovirens* has been collected recently in the Niassa Province of northwestern Mozambique (*Burrows 11154* & *11171*, BNRH).

Until now the circumscription of *M.* sect. *Buxifolia* has included ten species (Stone, 2014). In South Africa there are two species, *M. bachmannii* and *M. natalense*, according to recent treatments (Coates-Palgrave, 2002, Germishuizen et al., 2006, Boon, 2010). *Memecylon bachmannii* occurs near the coast in Pondoland (Eastern Cape) and southern KwaZulu-Natal, while *M. natalense* inhabits somewhat drier forests of the same region and has a wider but sporadic distribution northwards to Mpumalanga and Limpopo. The range of *M. natalense* has also been reported to extend to northern Mozambique and southern Malawi (Fernandes and Fernandes, 1978; 1980).

Evolutionary relationships in southern African *Memecylon* were recently investigated with population-level sampling and comparative sequencing of the nuclear rDNA ITS and 5’ ETS regions (Stone et al., 2017a). That study has clearly shown that *M. natalense* as previously circumscribed is not a monophyletic group and includes some geographically outlying populations warranting recognition as distinct taxa. The present study is a morphological study and revision of the *Memecylon natalense* species-complex (Mona and Stone, 2016). However, in the meantime, four new species of *M.* sect. *Buxifolia* were described, so that their names would be available for a recently published book by Burrows et al. (2018).

In this chapter, we compare geographic distribution and morphology between *M. natalense* and the six presently recognized species of *M.* sect. *Buxifolia* in Mozambique, and provide an identification key to the seven currently recognized species of Mozambican *Memecylon*. In the species descriptions, if a single measurement is given it refers to the length of the character. Alternatively, if measurements are separated by “×” the first measurement (s) refers to the length of the character and the second measurement (s) refers to the width of the character, this format is also followed in chapter 6. The extent of occurrence (EOO) and area of occupancy (AOO) were estimated using GeoCAT (Bachman et al., 2011), and the conservation status of each species is evaluated according to the IUCN Red List Categories and Criteria (IUCN, 2012).

Instead of presenting a single taxonomic chapter, the formal treatment of species has been divided into two separate manuscripts each intended for journal publication. The treatment of the Mozambican species (Chapter 5) was prepared so that the names of several new species could be effectively and validly published under the internationally recognised rules of botanical nomenclature (see Turland et al., 2018 for the most recent revision). This was done to make the species-names 'available' for use in a recently published book on the *Trees and Shrubs of Mozambique* (John Burrows et al., 2018).

5.2 Taxonomy

5.2.1. *Memecylon incisilobum* R.D. Stone & I.G. Mona (in Stone et al., 2017b, Fig. 5.1)

Type:—MOZAMBIQUE. Prov. Gaza: forest surrounding M-cel tower 11 km from Bilene on road to Macia, elevation 60 m, 25°11'31"S, 33°12'33"E, 28 October 2015, *Burrows et al. 14765* (holotype BNRH!, isotypes CAS, K, LMA, MO, NH, NU!, PRE).

Evergreen understory tree up to 7 m; bark brownish gray, longitudinally fissured; young branchlets slender, quadrangular to narrowly quadrangular-alate; older branchlets terete, whitish gray, longitudinally fissured; nodes thickened; internodes between normal leafy nodes (20–) 30–50 (–60) mm. Leaves subcoriaceous, dark green and glossy above, somewhat paler below; petioles 2.5‒3 mm; leaf-blades elliptic, (45–) 50–70 (–85) × (18–) 25–35 (–45) mm, cuneate at base (margins curved slightly inwards) and confluent with the petiole, ± broadly and obtusely acuminate at apex, acumen (3–) 4.5–8.5 (–11) mm (sometimes indistinct or with apex acute); midnerve clearly visible, impressed on the upper surface, ± prominent on the lower (especially toward the leaf base); one pair of lateral nerves faintly visible on both surfaces, curvilinear and 1.5‒4 mm from the margin in the basal half of blade; transverse veins ca. 5 pairs, faintly visible, oblique relative to the midnerve, prominent on both upper and lower surfaces in dried material. Cymes 1‒9-flowered, solitary (rarely geminate) at defoliated nodes of older branchlets, less often in the leaf axils and at bracteate nodes alternating with those bearing fully developed leaves, occasionally borne terminally; peduncles (3–) 5–10 (–13) mm; secondary axes slender, 1–5 in number, mostly 3.5‒7 mm; additional axes when present mostly 3‒5.5 mm; bracts rapidly deciduous. Flowers borne individually at the ends of inflorescence axes, pedicels 1‒2 (‒3) mm; hypantho-calyx green, broadly cupuliform, 2‒2.5 × 5 mm, margin shallowly sinuate; lobes broadly rounded, each with scarious margin regularly incised ± to the base, together forming a ring of 8 whitish, deltoid-acute teeth ca. 1 mm high; corolla in bud sharply apiculate (apiculum ca. 1 mm; petals white, broadly ovate to rhombiform, 4 × 3 mm, truncate at base above the short claw ca. 0.5 mm, midnerve impressed on the adaxial surface, prominent on the abaxial surface forming a keel that extends at the apex into a sharp acumen ca. 1 mm; staminal filaments 4 mm; anthers dolabriform, 1.25–1.5 × 0.75–1 mm, connective with thecae positioned at the anterior end, strongly incurved by the dorsal oil-gland; style ca. 7 mm; epigynous chamber with membranous partitions forming a V-shaped structure beneath each petal and with a low, non-membranous ridge radiating from the base of style towards each episepalous stamen. Fruits baccate, 1-seeded, green before maturity, subglobose, 5–7 mm in diameter, crowned by the persistent calyx 1.5–2 mm, thickened and collar-like with lobes curved inwards partially concealing the epigynous chamber; scarious teeth on calyx margin not persistent or only partially so.

Additional specimens examined (paratypes):—MOZAMBIQUE. Gaza province.: M-cel tower, ± 10 km from Bilene on road to Macia, elevation 70 m, 24 July 2005, *Burrows 9050* (BNRH!); next to M-cel tower 10 km from Bilene on road to Macia, elevation 67 m, 25°11'31"S, 33°12'36"E, 11 December 2009, *Burrows et al. 11512* (BNRH!, NU!); M-cel tower forest, ca. 11 km from Bilene beach to Macia, 25°11'31"S, 33°12'31"E, elevation 61 m, 17 March 2016, *Matimele & Tokura 2208* (BNRH, LMA, NU!).

Distribution and habitat:—Known only from the type locality in Gaza Province, southern Mozambique, about 10 km inland from Praia do Bilene (Stone et al., 2017b; Fig. 5.3). Small remnant of tall coastal forest occupying the slopes of a low sand hill (ancient dune) at 60–70 m elevation. In March 2016 there were 42 individuals of *M. incisilobum* counted (according to the collection-label of *Matimele & Tokura 2208*).

Phenology:—Flowers in late October. Immature fruits found in mid-March.

Conservation status:—*Memecylon incisilobum* is known from a single location and has an extent of occurrence (EOO) and area of occupancy (AOO) of 0.005 km^2 or less. According to Matimele (2016), the species is threatened by forest clearing for subsistence agriculture, wood-cutting for charcoal production, and runaway fires. For these reasons, Matimele (2016) has assessed *Memecylon incisilobum* (called *Memecylon* sp. nov.) as Critically Endangered [CR A3cd; B1ab(i, ii, iii, v)+2b(iii); C2a(ii)] following the IUCN Red List Categories and Criteria (IUCN 2012).

Etymology:—The epithet *incisilobum* is an adjective referring to the incised calyx-lobes, this being one of the main features distinguishing this species from *M. natalense*.

Discussion:—*Memecylon incisilobum* has formally been described by Stone et al. (2017b) and is closely related to another new species, still undescribed, that is known from a single locality in the Kosi Bay Nature Reserve, northeastern KwaZulu-Natal, South Africa. The two populations are separated by an airline distance of ca. 200 km, yet their nrDNA spacer sequences, obtained from the samples *Burrows et al. 11512* (BNRH) and *Styles 3539* (NH), have 100% identity with respect to each other, seemingly an indication of recent divergence. Molecular phylogenetic analyses suggest that the Gaza and Kosi Bay populations are more closely related to the Mt Mulanje population in southern Malawi (described below as *M. nubigenum* R.D. Stone & I.G. Mona) than they are to typical *M. natalense* sampled further to the south in KwaZulu-Natal (Stone, 2014, Stone et al., 2017a). In the present study, we have found that the Gaza and Kosi Bay populations share the features of calyx-lobes with scarious margin and yellow anther connectives, which clearly sets them apart from *M. natalense* in which the calyx-lobes remain subcoriaceous throughout and green (sometimes suffused with dark purple) and the anther connectives are white.

Morphologically, *M. incisilobum* is clearly distinguished from the Kosi Bay *Memecylon* by its cymes solitary or rarely geminate (versus cymes solitary or in fascicles of 2‒3); longer inflorescence axes, peduncles mostly 5–10 mm (versus 3–5 mm); secondary axes mostly 3.5‒7 mm (versus 2‒3 mm); more numerous flowers up to 9 flowers per cyme (versus flowers mostly 1‒3, rarely 4 or 5 per cyme); hypantho-calyx differently shaped, broadly cupuliform (versus obconic to cupulo-patellate); calyx-lobes with scarious margin ca. 1 mm high and regularly incised ± to the base (versus scarious margin ca. 0.5 mm high and irregularly erose-denticulate or occasionally with one lobe shallowly incised); corolla in bud sharply apiculate with apiculum ca. 1 mm high (versus rounded-apiculate); shorter styles ca. 7 mm (versus 8‒10 mm); and fruits with calycinal crown thickened and collar-like with lobes curved inwards (versus calycinal crown not thickened and collar-like, lobes erect). There also seems to be a difference in their respective flowering times late October for *M. incisilobum* (versus early December for the Kosi Bay *Memecylon*).

Memecylon incisilobum differs from *M. natalense* by its elliptic leaf-blades with transverse veins prominent on both surfaces in dried material (versus leaf-blades broadly elliptic-ovate with transverse veins ± obscure especially on the lower surface); cymes borne mostly at the defoliated nodes of older branchlets (versus cymes mostly axillary the bracteate nodes alternating with those bearing fully developed leaves); peduncles mostly 5–10 (–13) mm and up to 9-flowered (versus peduncles mostly 0.5–5 mm and 1−4-flowered); hypantho-calyx broadly cupuliform with calyx-lobes scarious and regularly incised ± to the base (versus hypantho-calyx obconic, the margin slightly and obtusely 4-lobed); corolla in bud sharply apiculate (versus corolla in bud rounded); anther connectives yellow (versus white); and fruits with calycinal crown thickened and collar-like with lobes curved inwards (versus calycinal crown not thickened and collar-like, lobes spreading) (Stone et al., 2017b; Table 5.1).

In comparison to *M. insulare* it has a larger stature, a tree to 7 m (versus a shrub to 2 m); larger leaves, mostly 50–70 × 25–35 mm (versus 15–45 × 5–27 mm); ± broadly and obtusely acuminate apex (versus leaf apices obtuse to rounded); transverse veins faintly visible on both surfaces (versus transverse veins obscure); somewhat larger flowers hypantho-calyx 2–2.5 × 5 mm (versus 2 × 3.5 mm); petals bigger 4 × 3 mm (versus smaller petals 3.5 × 2.5 mm). However, *M. incisilobum* and *M. insulare* are rather similar in their inflorescence dimensions, 1–9-flowered (up to 12-flowered in *M. insulare*); acutely apiculate shape of the corolla in bud, and in having petals keeled on the back (Stone et al., 2017b; Table 5.1).

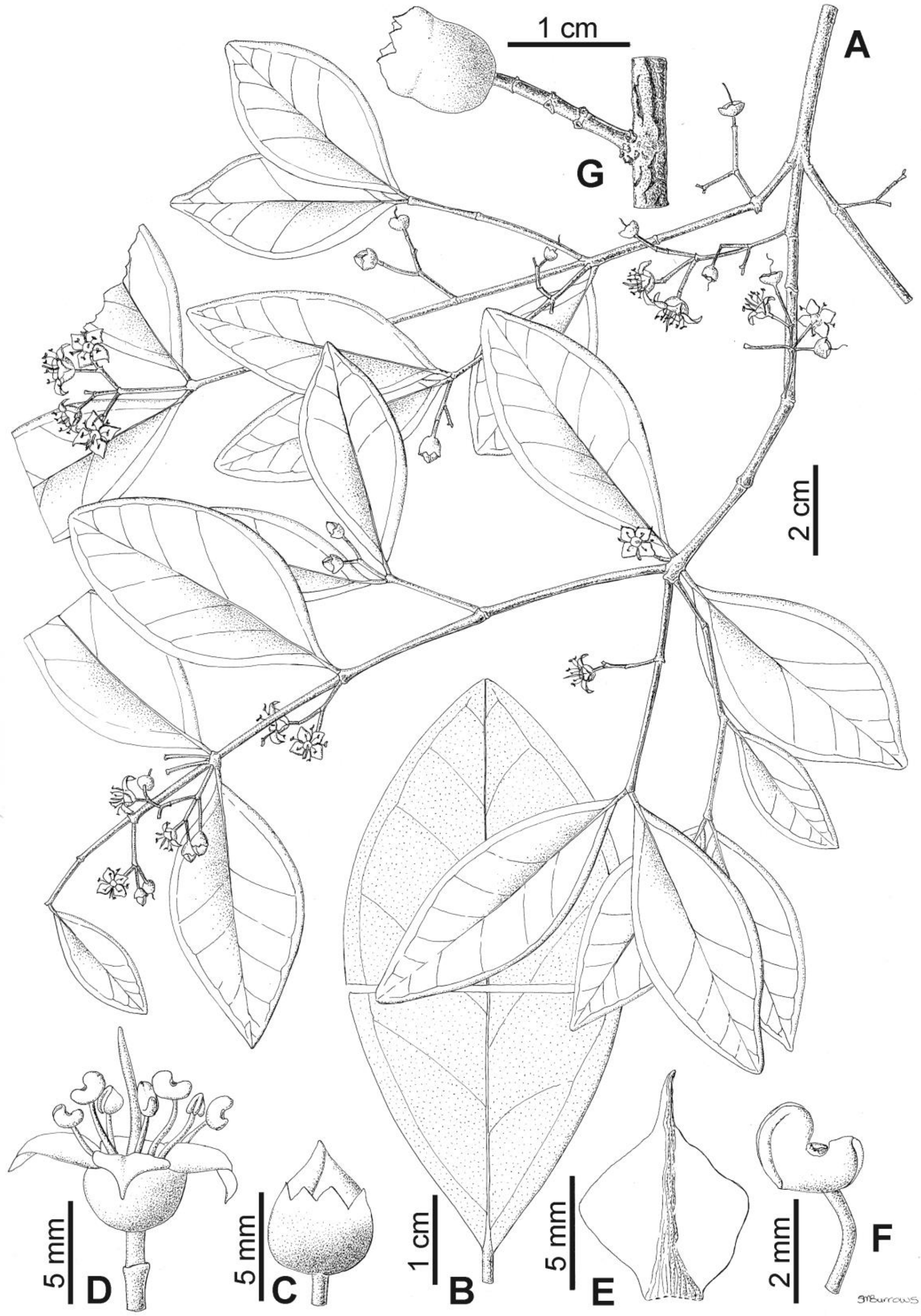


Figure 5.1. *Memecylon incisilobum.* **A.** Flowering branch. **B.** Leaf. **C.** Floral bud. **D.** Open flower. **E.** Petal. **F.** Stamen. **G.** Fruit. (**A–F** from *Burrows 14765*, BNRH; **G** from *Matimele & Tokura 2208*, BNRH. Drawing by Sandie Burrows, reproduced from Stone et al., 2017b).

5.2.2. ***Memecylon nubigenum*** R.D. Stone & I.G. Mona in Stone et al. (Stone et al., 2017b: 158; Fig. 5.2.)

Type:—MOZAMBIQUE. Prov. Nampula: Ribáuè, serra Mepáluè, elevation ca. 1600 m, 09 December 1967, *Torre* & *Correia 16431* (holotype LISC!, isotypes COI, K!, LMU!, PRE!, SRGH).

Evergreen understory tree 4‒7 (‒17) m tall. bark brownish gray; youngest branchlets brown to dark brown, strongly quadrangular and ± narrowly alate; older branchlets eventually becoming terete, grayish brown to grayish white, ± longitudinally fissured; nodes thickened; internodes (10–) 18–32 (–45) mm. Leaves subcoriaceous, dark green on the upper surface, paler beneath; petioles 1‒3 (–4) mm; blades ovate, varying to ± elliptic, (25–) 35–50 (–60) × (12–) 18–25 (–32) mm, cuneate to rounded at base, ± broadly acuminate at apex, acumen up to 8 mm, obtuse varying to rather acute or sometimes indistinct, margins narrowly and shallowly revolute; midnerve clearly visible, impressed on upper surface, prominent on lower (especially toward the leaf base); intramarginal nerves faintly visible on upper surface; transverse veins 4–5 pairs, oriented at an oblique angle relative to midnerve, obscure or ± faintly visible on the upper surface in dried material. Cymes ca. 15 mm, 1–3-flowered, solitary to geminate or in fascicles of 2, borne at the defoliated nodes of older branchlets, in the leaf axils and at the bracteate nodes alternating with those bearing fully developed leaves; peduncles 1–7 (–11) mm; secondary axes 1–6 mm; bracts rapidly deciduous. Flowers borne individually at the ends of inflorescence axes, on pedicels 1–3.5 mm; hypanthocalyx ca. 2.5 × 3.75 mm, obconic; lobes broadly rounded, ca. 0.5 × 2 mm, green and subcoriaceous with a very narrow scarious margin; corolla in bud distinctly apiculate, subacute at apex; petals white, subrhombic, 5 × 4 mm, acute at the apex; staminal filaments ca. 6 mm; anthers ca. 2.5 mm, connective strongly incurved by the dorsal oil-gland; ovules 2–8; style 10 mm. Fruits baccate, 1-seeded, green becoming black at maturity, subglobose, 7–8 × 7–8 mm in diameter, crowned by the persistent calyx ca. 1 mm; epigynous chamber lacking radial partitions, marked only by scars of deciduous petals, anthers and style.

Additional specimens examined (paratypes):—MALAWI. Southern Region: Mlanje District, Ruo Gorge, elevation ± 1000 m, 01 September 1970, *Müller 1474* (COI, K!, SRGH); Mulanje District, Ruo Gorge 2.5 km above Hydro Electric Station

[S side of Mulanje Mt.], elevation 1250 m, 07 May 1980, *Blackmore et al. 1512* (K!, MAL); Mulanje Mt. District, Lichenya Forest (Mim-Mim path), elevation 1820 m, 29 September 1983, *Dowsett-Lemaire 1026* (BR); Mulanje Mt. District, Great Ruo Gorge, elevation 1250 m, 23 June 1984, *Dowsett-Lemaire 1159* (BR!); Mt. Mulanje, Pamba Gorge at Savani stream crossing, elevation 1250 m, 30 September 1986, *Chapman 8098* (K!, MO!, PRE!); Mt. Mulanje, Chisongeli Forest (West), elevation 1500 m, 15 September 1988, *Chapman 9292* (K!, MO!, PRE!, WAG!); Mulanje District, Lujeri Power Station, above Lujeri Dam, along Ruo River, elevation 1137 m, 15°57'16.15"S, 35°11'16.83"E, 13 July 2007, *Nothale & Patel 171* (K!). **MOZAMBIQUE. Zambézia province.:** Guruè, encosta da serra do Guruè via fábrica Junqueiro a Oeste dos Picos Namúli, próx. do rio Malema, elevation *ca.* 1700 m, 06 November 1967, *Torre & Correia 15956* (COI, EA, K!, LISC, SRGH).

Distribution and habitat:—Known from two granitic inselbergs in northern Mozambique, i.e., the Namúli massif (Zambézia province) and Monte Mepáluè (Nampula province), in cloud forest at 1600–1700 m elevation (Stone et al., 2017b; Fig. 5.3). The collecting localities of Torre and Correia in November 1967 were on the eastern side of the Namúli massif, on slopes and in riverine forests of Mt Namúli (Timberlake et al., 2009).

Also known from the Mulanje massif, a granitic inselberg in southern Malawi, at elevations of 1000–1800 m, in forests classified as either "mid-altitude" or "submontane" (Dowsett-Lemaire, 1988). At Mulanje, most collections of *M. nubigenum* are from the Ruo Gorge at the southern end of the massif, with other forested localities represented by single collections (Lichenya Plateau, Chisongeli, Pamba Gorge).

Phenology:—Flowers in December. Fruiting collections in May–July, also in September and November.

Conservation status:—*Memecylon nubigenum* is known from six locations including two in northern Mozambique and four in southern Malawi (Mulanje massif). It has an EOO of ca. 5,900 km^2 and an AOO of 24 km^2 (assuming a 4 km^2 grid cell size). In Mozambique, the type locality in Nampula Province is formally protected in the Mepáluè [M'páluè] Forest Reserve which has a reported area of 42.5 km^2 (Faye, 2005). At the base of the mountain, the village of Ribáuè lies in a densely populated valley.

Natural vegetation on the lower slopes has already been converted to subsistence agriculture, but human intrusion at the higher elevations (above 1100 m) is impeded by steep slopes and lack of road access (Müller et al., 2005). The second Mozambican location, in the Namúli massif near Guruè (Zambézia province), is not formally protected but has been recommended for such status (Timberlake et al., 2009). Much of the natural vegetation below 1500 m elevation has already been transformed, but ca. 10 km^2 was covered by montane forest at elevations of 1600–1900 m (determined from 2005 Landsat imagery). Major threats in forested habitats above 1400 m include potato cultivation, frequent wildfires, and logging.

The locations in Malawi are protected in the Mulanje Mountain Forest Reserve, first gazetted in 1927 but with later boundary adjustments due to on-going human encroachment on the lower slopes. The massif is surrounded by villages of the Mulanje and Phalombe districts, tea estates, and small-scale cultivation. According to Dowsett-Lemaire (1988), forest cover (estimated from aerial photographs) was 15 km^2 at middle elevations (900–1500 m) and 46 km^2 on the upper slopes and plateaux (1500–2300 m). Continuing threats include clearing of forest for subsistence agriculture and charcoal production, wildfires, extraction of the commercially valuable Mulanje cypress (*Widdringtonia whytei* Rendle), and spread of the naturalized Mexican weeping pine (*Pinus patula* Schiede ex Schltdl. & Cham.). Deforestation has been most severe on the southern and southeastern slopes of the massif, in or near areas where *M. nubigenum* has been collected in the past, i.e., Chisongeli and near the entrance to the Ruo Gorge (Dowsett-Lemaire, 1988). This trend of environmental deterioration and unsustainable resource exploitation led to the establishment of the non-governmental Mulanje Mountain Conservation Trust around 1994. This organization has attracted substantial funding from the World Bank and more recently the Norwegian government (Wisborg and Jumbe, 2010).

Memecylon nubigenum is thus provisionally assessed as Vulnerable [VU B1ab(iii)+B2ab(iii); D2] according to the IUCN Red List Categories and Criteria (IUCN 2012).

Etymology:—The epithet *nubigenum* is a compound derived from the Latin noun *nubis* meaning “cloud” and the verb *gignere* meaning “to be born.” It functions as an adjective and means “born of or originating from the clouds.” It is a reference to the habitat in mountains of northern Mozambique and southern Malawi.

Discussion:—The *Memecylon nubigenum* populations from mountains of northern Mozambique and southern Malawi (Mt Mulanje), were earlier identified as *M. natalense* (Fernandes and Fernandes, 1972; 1978; 1980) but are evidently not very closely related to that species (Stone et al., 2017a), clearly indicating the need to recognise them as a distinct taxon. It was formally described by Stone et al. (2017b). *Memecylon nubigenum* also differs morphologically from South African *M. natalense sensu stricto* in the shape of the obtuse leaf apex (versus acute apex), the shape of the corolla in bud is distinctly apiculate (versus rounded to subacute corolla in bud), and the shape of the fruits is strictly globose (versus ± ellipsoid or tending to be somewhat longer than wide) (Stone et al., 2017b; Table 5.2).

This species was previously illustrated by Fernandes and Fernandes (1972; *tabula* 2, as *M. natalense*).

Figure 5.2. *Memecylon nubigenum*. Image of the holotype (*Torre* & *Correia 16431*, LISC). Source: Herbario, Instituto de Investigação Científica Tropical, Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Portugal (reproduced from Stone et al., 2017b).

5.2.3. *Memecylon rovumense* R.D. Stone & I.G. Mona in Stone et al. (Stone et al., 2017b: 160, Fig. 5.3.)

Type:—TANZANIA. Lindi Region: Lindi District, Chitoa Forest Reserve, elevation 240–420 m, 9°58'S, 39°27'E, 18 June 1995, *Clarke 56* (holotype K!).

Evergreen shrub or understory tree up to 6 m tall; young branchlets quadrangular (subquadrangular below the "aphyllous" nodes); nodes thickened; internodes between normal leafy nodes (10–) 25–65 (–110) mm; bracts of the "aphyllous" (i.e., inflorescence-bearing) nodes lanceolate, ca. 3 mm, rapidly deciduous. Leaves coriaceous, on petioles 1–3 (–4) mm; blades elliptic to ± ovate or obovate, (25–) 35–55 (–70) × (13–) 18–33 (–40) mm, cuneate at base, ± broadly and obtusely acuminate at apex, the acumen (1–) 2–4 (–5.5) mm or sometimes indistinct with the leaf apex then rounded and obtuse; midnerve clearly visible, impressed on the upper surface, ± prominent on the lower (especially toward the leaf base); intramarginal nerves faintly visible; transverse veins 3–5 pairs, oriented at an oblique angle relative to the midnerve, faintly visible in dried material. Cymes 1–3 (–4)-flowered, solitary to geminate or in fascicles of 2 (–3), borne at the defoliated nodes of older branchlets, less often in the leaf axils and at the bracteate nodes alternating with those bearing fully developed leaves; peduncles 1.5–2 mm; secondary axes ± absent, the flowers thus directly subumbellate; bracts ca. 2 mm, ± lanceolate, narrowed to the base, rapidly deciduous. Flowers in bud on very short pedicels, corolla rounded-apiculate; fully developed and open flowers not seen. Fruits baccate, 1-seeded, green before maturity, broadly pyriform, 18 × 14 mm, conspicuously verrucose-wrinkled, lacking a calycinal crown but with lobes persistent, broadly deltate and ca. 1 mm, curved inwards partially concealing the epigynous chamber.

Additional specimens examined (paratypes):—MOZAMBIQUE: Cabo Delgado province: Namacubi (Banana) Forest west of Quiterajo, elevation 90 m, 11°45'55"S, 40°23'45"E, 25 November 2008, *Burrows 10766* (BNRH!, K!); Quiterajo, elevation 110 m, 11°45'48.24"S, 40°21'47.16"E, 24 November 2009, *Luke 13891* (EA!, K!, LMA, P); Namacubi Forest near Quiterajo, elevation 90 m, 11°45'23"S, 40°24'00"E, 08 September 2014, *Timberlake & Massingue s.n.* (NU!).

TANZANIA. Lindi Region: Chitoa Forest, elevation 415 m, 05 December 2001, *Mbago et al. 2266* (DSM, K!); Kilwa District, ca. 1 km W of Miteja soccer pitch, elevation 50 m, 08°16'14"S, 39°13'36"E, 03 August 2003, *Kayombo et al. 4431* (CAS!, MO); Ngarama North Forest Reserve, elevation 420 m, 09°24'S, 39°19'E, 26 November 2003, *Luke & Kibure 9741* (CAS!, EA!, MO).

Distribution and habitat:—Known from three locations in southern Tanzania (Lindi Region) and one location in northern Mozambique (Namacubi Forest near Quiterajo, Cabo Delgado Province) (Stone et al., 2017b; Fig. 5.3). Found in coastal dry forest at elevations of 50–420 m.

Phenology:—Floral buds in late November; and fruits in June.

Conservation status:— *Memecylon rovumense* is known from four locations including three in southeastern Tanzania (Lindi Region) and one in northern Mozambique (Cabo Delgado Province). It has an EOO of ca. 8,400 km^2 and an AOO of *ca.* 24 km^2 (assuming a 4 km^2 grid-cell size).

The coastal forests of East Africa are small and highly fragmented, most of them being less than 50 km^2 in size (Burgess et al., 2000). They are thought to be remnants of a more extensive forest cover that existed prior to the spread of dry climate in this region beginning *ca.* 16 Million of years ago (Jacobs, 2004). However, recent disturbance by human activities (especially increased fire frequency) has also contributed to the reduction and fragmentation of these forests (Burgess et al., 1998).

In Tanzania, *M. rovumense* currently receives an uncertain level of protection, despite of the two of the three known locations lying within gazetted forest reserves. This is because the management budgets and staffing levels are extremely low (Burgess et al., 2012). The Chitoa Forest Reserve, which includes the type locality, is ca. 45 km west of the coastal town of Lindi. It is a small reserve (7.7 km^2) with only 1.8 km^2 designated as “protective” forest and the remaining 5.9 km^2 as “production” forest intended for sustainable use (Clarke, 1995; Burgess et al., 2012). In total, the Chitoa Plateau and nearby Litipo Forest Reserve contain an estimated 8 km^2 of mixed dry forest (Prins and Clarke, 2007). The Chitoa Forest Reserve is located 3 km away from the nearest villages and is only accessible by footpath; this suggests that threats to the forest may be limited, although Clarke (1995) noted some wood cutting of poles by local people and the possibility of uncontrolled bushfires. About 65 km further to the north, the Ngarama North Forest Reserve is larger (ca. 45 km^2) with 15 km^2 designated as “protective” forest and the remainder as “production” (Burgess et al., 2012). The reserve is situated on the Ruwawa Plateau largely covered by “scrub forest” over coral rag limestone, but with 13 km^2 of mixed dry forest and legume-dominated dry forest (Prins and Clarke, 2007). Threats are minimal because of low human population density in the area, although some timber poaching has been observed (Prins and Clarke, 2007). The remaining coastal forests of the Lindi Region (SE Tanzania) are also threatened by recent improvements in road infrastructure, which are opening up previously remote and relatively inaccessible areas for logging and charcoal production (Prins and Clarke, 2007; Burgess et al., 2012).

In Mozambique, the only known location of *M. rovumense* is not in a protected area. Ongoing threats in the Namacubi Forest include continued clearing for subsistence agriculture, cutting for poles, uncontrolled fires, and possible road construction for oil-and-gas development which would increase access to and clearing of the forest (Timberlake et al. 2011; Cheek and Darbyshire, 2014).

Memecylon rovumense is thus provisionally assessed as Endangered [EN B1ab(iii)+B2ab(iii)] according to the IUCN Red List Categories and Criteria (IUCN 2012).

Etymology:—The epithet *rovumense* is an adjective used to indicate geographical origin, i.e., to emphasize that the new species is an endemic of the Rovuma region of northern Mozambique and southeastern Tanzania. The region itself gets its name from the Rovuma River which forms the border between these two countries.

Discussion:—*Memecylon rovumense* has been previously confused with *M. natalense* and formally described by Stone et al., (2017b), but DNA evidence suggests it may have originated through hybridization between a lineage close to the Kenyan *M. fragrans* A. Fernandes and R. Fernandes (Fernandes and Fernandes, 1960) and another, as-yet unidentified Mozambican lineage close to *M. torrei* (Stone et al., 2017b). Its fruits are quite distinctive in being relatively large, yellow-green and warty-roughened on the exterior, appearing much like miniature avocados, seen in the collection *Clarke 56* (K).

It differs from South African *M. natalense* by its more thickly coriaceous leaves that are rounded and obtuse to ± broadly obtuse-acuminate at the apex (versus thinly coriaceous with acumen acute apex); cymes borne mostly at the defoliated nodes of older branchlets (versus cymes mostly axillary and at the bracteate nodes alternating with those bearing fully developed leaves); larger, broadly pyriform and conspicuously verrucose-wrinkled fruits lacking a persistent calycinal crown (versus fruits up to 10 mm in diameter, ellipsoid to subglobose with smooth exterior and calycinal crown conspicuous) (Stone et al., 2017b; Table 5.1).

In comparison to the Kenyan *M. fragrans* it has broader, differently shaped leaves mostly 33–55 × 17–33 mm and ± elliptic (versus 20–55 × 10–24 mm and ± ovate), and the cymes are borne mostly at the defoliated nodes of older branchlets (versus cymes mostly axillary and at the bracteate nodes alternating with those bearing fully developed leaves). The fruits of *M. fragrans* are also smaller and differently shaped (versus ovate to elliptic, 8–9.5 × 6–7 mm with exterior only slightly roughened and calycinal crown conspicuous).

In comparison to the Mozambican *M. torrei* it has somewhat smaller leaves mostly 33–55 × 17–33 mm (versus 40–70 × 20–40 mm), and the lower leaf surface is pale green (versus vivid yellowish green) (Stone et al., 2017b; Table 5.1). The fruits of *M. torrei* are similarly large (*ca.* 18 × 14 mm) and also with exterior warty-roughened, seen in the collection *Goyder et al. 6107* (P).

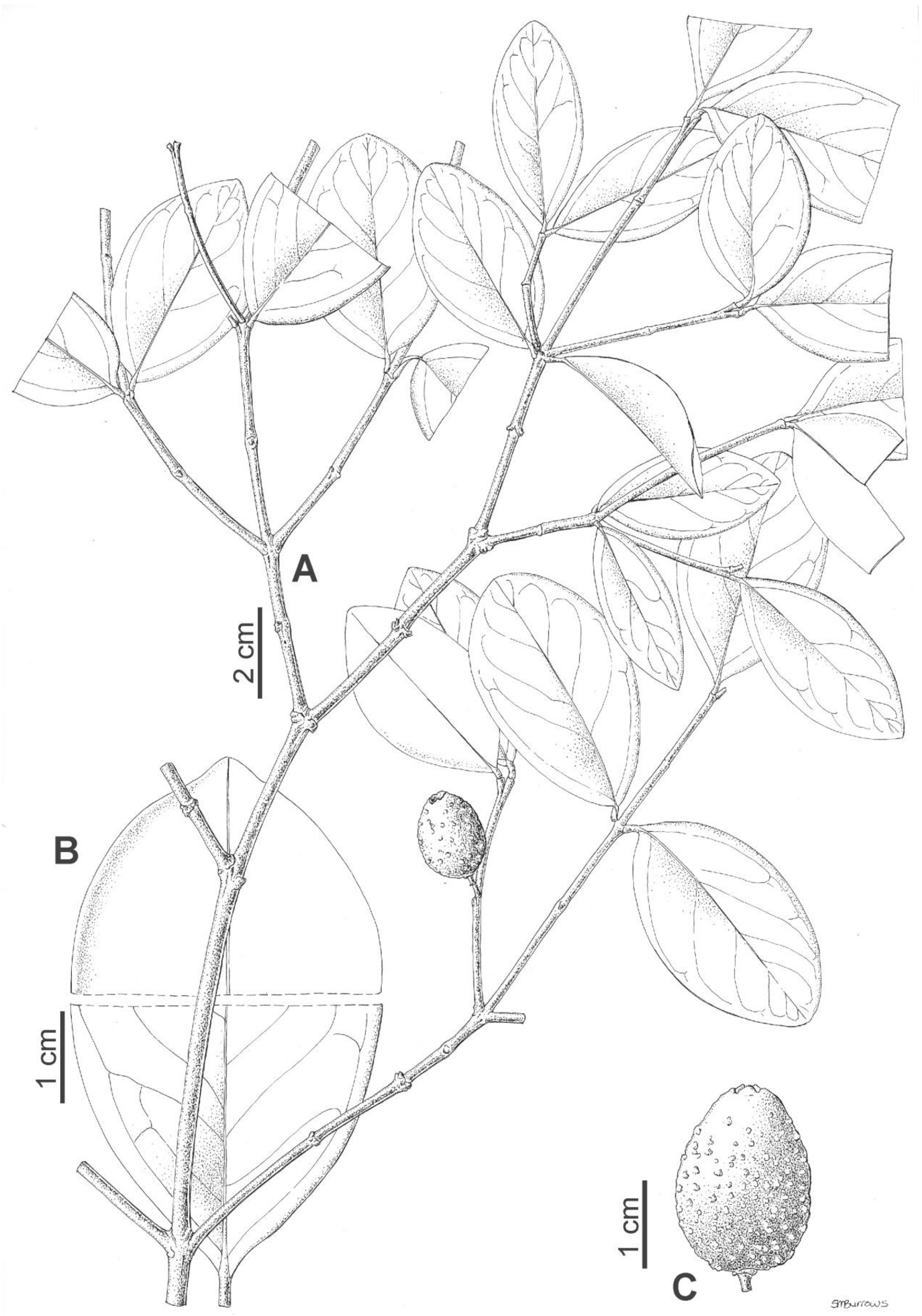


Figure 5.3. *Memecylon rovumense*. **A.** Fruiting branch. **B.** Leaf. **C.** Fruit. (**A**–**C** from

Clarke 56, K. Drawing by Sandie Burrows, reproduced from Stone et al., 2017b).

5.2.4. ***Memecylon aenigmaticum*** R.D. Stone in Stone et al. (Stone et al., 2017b: 163, Fig. 5.4.)

Type:—MOZAMBIQUE. Cabo Delgado: Macomia district, Quiterajo, Namparamnera forest, elevation 136 m, 11°49'02.9"S, 40°20'31.7"E, 29 November 2008, *Timberlake et al. 5574* (holotype K!, isotypes LMA, P!).

Evergreen shrub to 3 m high; bark brown; young branchlets whitish grey, quadrangular, soon becoming terete with age; nodes thickened; internodes between normal leafy nodes 10–35 (–65) mm. Leaves thickly coriaceous, petioles 1−2 mm; blades obovate, 17.5–30 × 10–17.5 mm, cuneate at base, rounded to obtuse at apex; only the midnerve clearly visible, impressed on the upper surface, ± prominent on the lower (especially toward the leaf base); intramarginal nerves and transverse veins ± obscure. Flowering cymes and flowers not seen. Fruits baccate, 1-seeded, solitary at the defoliated nodes of older branchlets, in the leaf axils and at the bracteate nodes alternating with those bearing fully developed leaves, borne on a very short, stout axis (length ca. 2 mm), pale green before maturity, elliptic to obovoid in outline, 9−10.5 × 7−8 mm, conspicuously verrucose-wrinkled; calycinal crown very short (ca. 0.3 mm high), margin sinuate to ± truncate.

Distribution and habitat:—Known only from the type collection made in Cabo Delgado Province, northern Mozambique (Stone et al., 2017b; Fig. 5.3). Found in coastal dry forest at 136 m elevation.

Phenology:—Flowers unknown; fruits in November.

Conservation status:—*Memecylon aenigmaticum* is known from a single location with an area of occupancy (AOO) of 4 km^2 (assuming a 4 km^2 grid cell size). Coastal forests in Cabo Delgado are virtually unprotected, and those in the Quiterajo vicinity are threatened by clearing for subsistence agriculture, logging of large timber trees and cutting of poles, and uncontrolled fires (Timberlake, 2009; Timberlake et al., 2011). *Memecylon aenigmaticum* is thus provisionally assessed as Critically Endangered [CR B2ab(iii)] according to the IUCN Red List Categories and Criteria (IUCN 2012).

Etymology:—The epithet *aenigmaticum* is an adjective based on the Greek noun *ainigma* meaning mysterious or difficult to interpret or understand. It is in reference that this new species is being previously confused with both *M. natalense* and *M. rovumense* (q.v.).

Discussion:—This species was formally described in Stone et al. (2017b), *Memecylon aenigmaticum* has been confused with the South African *M. natalense* but differs by its more thickly coriaceous leaves that are obovate in outline and rounded to obtuse at the apex (versus thinly coriaceous leaves, ovate in outline with apex acutely acuminate); cymes borne mostly at the defoliated nodes of older branchlets (versus cymes mostly axillary and at the bracteate nodes alternating with those bearing fully developed leaves); and by its ellipsoid to obovoid, verrucose-wrinkled fruits lacking a persistent calycinal crown (versus fruits ellipsoid to subglobose with smooth exterior and conspicuous calycinal crown) (Stone et al., 2017b; Table 5.1).

This new species appears closely related to *M. rovumense*, but differs by its much smaller leaves 17.5–30 × 1–17.5 mm (versus bigger leaves 33–55 × 17–33 mm) and differently shaped smaller fruits that are ellipsoid to obovoid and 9−10.5 × 7−8 mm (versus ovoid to broadly pyriform fruits, 18 × 14 mm) (Stone et al., 2017b; Table 5.1).

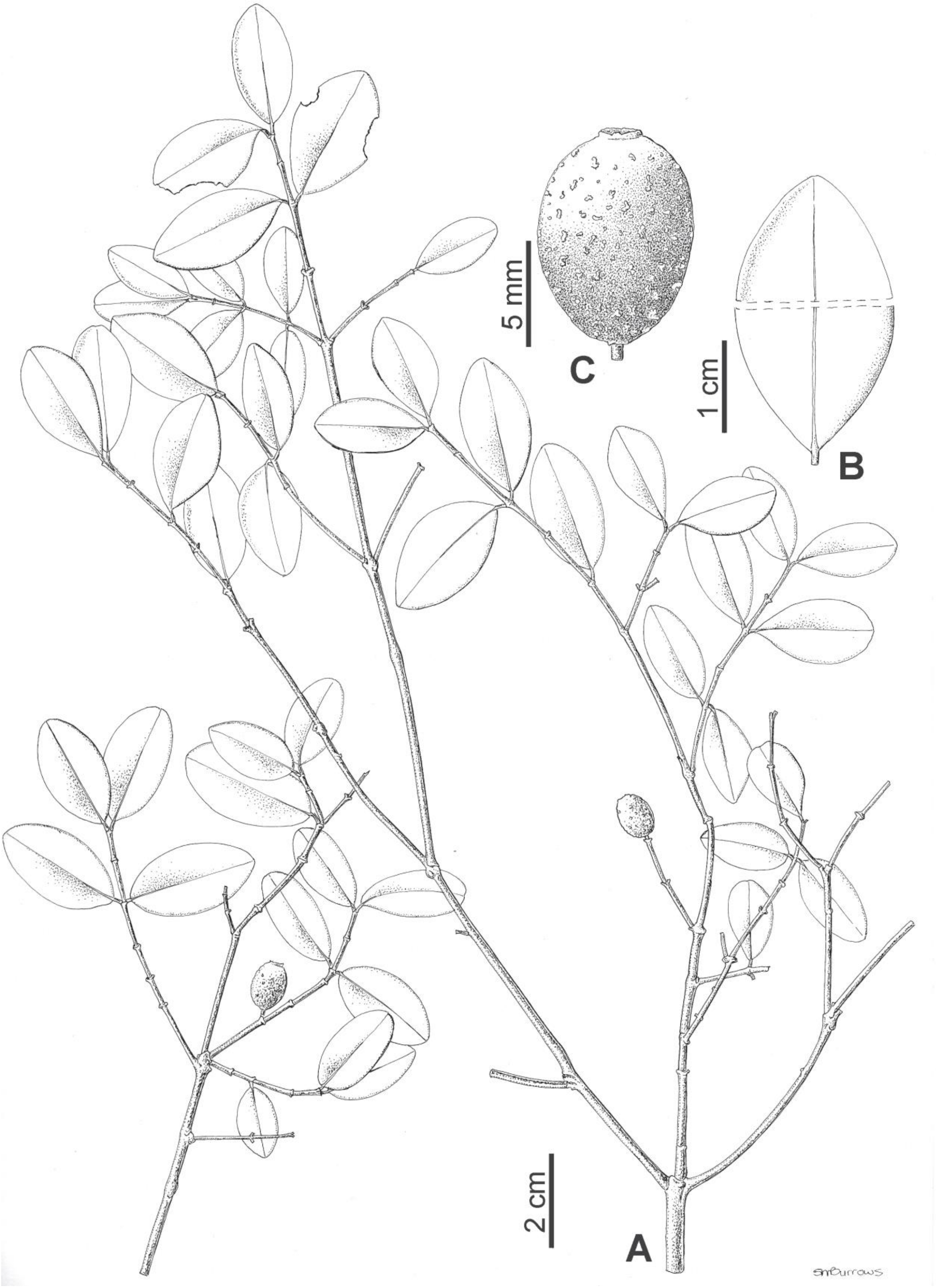


Figure 5.4. *Memecylon aenigmaticum*. **A.** Fruiting branch. **B.** Leaf. **C.** Fruit. (**A**–**C** from *Timberlake et al. 5574*, K. Drawing by Sandie Burrows, reproduced from Stone et al., 2017b).

Table 5.1. Comparison of geographic distribution and morphology between *Memecylon natalense* and the six presently recognized species of *M.* section *Buxifolia* in Mozambique

	M. natalense	***M. torrei***	***M. insulare***	***M. incisilobum***	***M. nubigenum***	***M. rovumense***	***M. aenigmaticum***
Distribution	South African endemic (in KwaZulu-Natal, Eastern Cape, Mpumalanga & Limpopo)	Coastal forests of N Mozambique (Nampula & Cabo Delgado provinces)	Magaruque Island near Vilanculos (Inhambane Province)	Coastal forest remnant near Praia do Bilene, S Mozambique (Gaza Province)	N Mozambique (Nampula & Zambézia provinces) & S Malawi (Mt. Mulanje) at 1000–1800 m elevation	N Mozambique, Namacubi coastal dry forest near Quiterajo (Cabo Delgado Province); also in S Tanzania (Lindi Region)	N Mozambique, Namparamnera coastal dry forest near Quiterajo (Cabo Delgado Province)
Habit	Small tree mostly 2–4 m (rarely to 15 m)	Shrub or small tree 1.5–3 m	Shrub to 2 m	Tree to 7 m	Tree 4–7 (–17) m	Shrub or tree to 6 m	Shrub to 3 m
Texture of leaves	Thinly coriaceous	Coriaceous	Coriaceous	Subcoriaceous	Subcoriaceous	Coriaceous	Thickly coriaceous
Leaf blades	Ovate, 30–60 × 15–30 mm	Elliptic to obovate, 40–70 ×20–40 mm	Elliptic to obovate, 15–45 × 15–27 mm	Elliptic, mostly 50–70 × 25–35 mm	Ovate to ± elliptic, mostly 35–50 × 18–25 mm	Elliptic to ± ovate or obovate, mostly 33–55 × 17-33 mm	Obovate, 17.5–30 ×10–17.5 mm
Leaf apex	Acutely acuminate	Obtuse to rounded	Obtuse to rounded	± broadly and obtusely acuminate	± obtusely acuminate	± broadly obtuse acuminate or rounded and obtuse	Rounded to obtuse
Transverse veins	± obscure, especially on the lower surface	Inconspicuous	Obscure	ca. 5 pairs, faintly visible, prominent on both surfaces in dried material	4–5 pairs, obscure or ± faintly visible on upper surface	3–5 pairs, faintly visible	± obscure

Lower leaf surface	Pale green	Vivid yellowish green	Yellowish green	Pale green	Pale green	Pale green	Pale green
Inflorescence position	Mostly axillary and at the intervening “aphyllous” nodes	Mostly axillary and at the intervening “aphyllous” nodes	Mostly axillary and at the intervening “aphyllous” nodes	Mostly at the defoliated nodes of older branchlets	At the defoliated nodes of older branchlets, in the leaf axils and at “aphyllous” nodes	Mostly at the defoliated nodes of older branchlets	At the defoliated nodes of older branchlets, in the leaf axils and at “aphyllous” nodes
Peduncles	Mostly 0.5–5 mm	ca. 2 mm	Up to 6 mm	Mostly 5–10 (–13)	1–7 (–11) mm	1.5–2 mm	ca. 2 mm
No. of flowers per inflorescence	1–4	1–3	up to 12	1–9	1–3	1–3 (–4)	(no data)
Hypanthocalyx	Obconical, ca.2.5 × 3.75 mm	Campanulate, 3 × 4 mm	Obconical, ca. 2 × 3.5 mm	Cupuliform, 2–2.5 × 5 mm	Obconical, ca. 2.5 × 3.75 mm	(no data)	(no data)
Calyx-lobes	Broadly rounded to triangular, 0.5–1 × 1.75–2 mm, green or suffused with dark purple	Broadly triangular, 1 × 2.5 mm	Broadly rounded to subtriangular, ca. 0.5 × 2 mm	Broadly rounded, ca. 1 mm high, scarious, regularly incised ± to the base	Broadly rounded, ca. 0.5 × 2 mm	(no data)	(no data)
Corolla in bud	Rounded to subacute	Rounded apiculate	Acutely apiculate	Sharply apiculate	Apiculate, subacute at apex	Rounded apiculate	(no data)

Key to the species of *Memecylon* in Mozambique

1. Bark thick, deeply longitudinally fissured; branchlets with all nodes bearing normal leaves; leaf apices rounded to truncate or emarginate; petals subdeltate-acuminate with apex sharply acute; anther connectives purple; fruits ovoid-ellipsoid, 12−14 × 6–8 mm. In Mozambique confined to “miombo” woodland in NW Niassa Province (*M.* sect. *Obtusifolia*) ....***M. flavovirens***

-. Bark thin, finely longitudinally fissured; branchlets with successive nodes alternating between normal leaves and reduced, often inflorescence-bearing bracts; leaf apices rounded to obtuse or ± acuminate; petals subrhomboid with apex rounded to subacute (acuminate in *M. incisilobum*); anther connectives whitish or yellow; fruits ± globose in some species, ovoid to ellipsoid or obovoid in others, 8−18 × 7−14 mm (*M.* sect. *Buxifolia*) 2

2. Leaf apices obtuse to rounded or ± broadly and obtusely acuminate, the acumen when present mostly 2–4 mm……………………………………………….….. 3

-. Leaf apices ± distinctly acuminate, the acumen 3–8.5 (−11) mm………………6

3. Leaf-blades 15−45 × 15−27 mm; cymes up to 12-flowered, on peduncles up to 6 mm long. Known only from Magaruque Island near Vilanculos (Inhambane Province) ……………………………………………………….... ***M. insulare***

-. Leaf dimensions as above or larger, 17.5−70 × 10−40 mm; cymes 1–3-flowered, on peduncles ca. 2 mm…...4

4. Leaf-blades 40–70 × 20–40 mm; lower leaf surface vivid yellowish green; fruits ovoid, 18 × 14 mm. Found in coastal forests of N Mozambique (Nampula and Cabo Delgado provinces) .... ***M. torrei***

-. Leaf-blades smaller 17.5–55 × 10−33 mm; lower leaf surface pale green; fruits as above or smaller, 9−18 × 7−14 mm..5

5. Leaf-blades mostly 35–55 × 18–33 mm; fruits ovoid to broadly pyriform, 18 × 14 mm. In Mozambique known only from the Namacubi coastal dry forest near Quiterajo (Cabo Delgado Province) ....***M. rovumense***

-. Leaf-blades 17.5–30 × 10–17.5 mm; fruits elliptic to obovoid, 9–10.5 × 7–8 mm. Known only from the Namparamnera coastal dry forest near Quiterajo (Cabo Delgado Province)..***M. aenigmaticum***

6. Leaf-blades elliptic, mostly 50–70 × 25–35 mm; cymes borne mostly at the defoliated nodes of older branchlets, on peduncles mostly 5–10 (–13) mm, up to 9-flowered; hypantho-calyx broadly cupuliform and with calyx-lobes scarious and regularly incised ± to the base; corolla in bud sharply apiculate; fruits with calycinal crown thickened and collar-like with lobes curved inwards. Coastal forest remnant in S Mozambique (Gaza Province) ....***M. incisilobum***

-. Leaf-blades ovate, dimensions ± smaller mostly 30–60 × 15–32 mm; cymes mostly axillary and at the bracteate nodes alternating with those bearing fully developed leaves, on peduncles 1–7 mm and usually 3-flowered; hypantho-calyx obconic, the margin slightly and obtusely 4-lobed; corolla in bud subacute; fruits with calycinal crown not thickened and collar-like, lobes spreading. Mountains of N Mozambique (Nampula and Zambézia provinces) at 1600–1700 m elevation……………………………………..………………...***M. nubigenum***

CHAPTER 6: REVISION OF SOUTH AFRICAN *MEMECYLON*

6.1. Introduction

Within the monophyletic, predominantly East African *Memecylon* section *Buxifolia* (Stone, 2014), previous authors had recognized two species in South Africa, viz. *M. natalense* Markgr. and *M. bachmannii* Engler (Van Wyk, 1983; Coates-Palgrave, 2002; Germishuizen et al., 2006; Boon, 2010). However, the morphological evidence and analyses presented in this study (see Chapters 2, 3 and 4), together with previous molecular results (Stone et al., 2017a), have clearly shown that the circumscription of *M. natalense* needs to be considerably narrowed, and that the species richness in southern Africa has been substantially underestimated. In this chapter, a formal taxonomic treatment is presented of the five currently recognised South African species, including updated descriptions of *M. natalense* and *M. bachmannii* and descriptions of three new, as-yet unnamed species. An updated key to the South African *Memecylon* species is also provided, as well as their conservation status.

Instead of presenting a single taxonomic chapter, the formal treatment of species has been divided into two separate manuscripts each intended for journal publication. The treatment of the Mozambican species (Chapter 5) was prepared so that the names of several new species could be effectively and validly published under the internationally recognised rules of botanical nomenclature (see Turland et al., 2018 for the most recent revision). This was done to make the species-names ‘available’ for use in a recently published book on the *Trees and Shrubs of Mozambique* (Burrows et al., 2018). Furthermore, the manuscript had to be prepared urgently because the book was already ‘in press’. Given the fact that the treatment of the Mozambican species (Chapter 5) was already published, it was logical to keep it separate from the revision of South African *Memecylon* (Chapter 6) so that the latter could also be submitted for publication. It should be further noted there are no species of *Memecylon* held in common between South Africa and Mozambique (hence there was no problem of having to treat the same species twice). Of course it would have been more desirable to complete a comprehensive revision of *Memecylon* section *Buxifolia*, but this would have been beyond the scope of an MSc project since the group in question includes other species from Tanzania, Kenya and Madagascar (some of these species already named but others still undescribed).

Species are the currency of biology (Agapow et al., 2004). Although most biological information is given with reference to "species" their definition remains controversial (Groves, 2001; Hausdorf, 2011). At the hub of taxonomist's problems, there is uncertainity of what kind of species concept to employ because they are numerous, and concepts vary in the criteria used to define species or species limits (Mayden, 1997). Why don't taxonomists agree on a single concept of species? Because many of these concepts and their associated definitions are incompatible, they are tailored for specific groups and have limited application elsewhere (De Queiroz, 2007). In most cases species are defined using a variety of different operational techniques (Agapow et al., 2004). Hence, I acknowledge that there is no single best species concept.

The main aim of the present study is to revise the *Memecylon natalense* species-complex. Species delimitations are based on the "diagnostic species concept," where species are defined as the smallest cluster of organisms possessing at least one diagnostic (i.e., unambiguous) character (Cracraft, 1989). Thus, taxa that are morphologically distinct are regarded as species. If measurements are separated by "×" the first measurement (s) refers to the length of the character and the second measurement (s) refers to the width of the character

6.2. Taxonomic treatment

6.2.1. *Memecylon natalense* Markgr.

Memecylon natalense Markgr. in Mildbraed (1934: 1078).

Homotypic synonym: — *Memecylon australe* Gilg & Schlechter in Schlechter (1907: 94), *nom. illeg.*; not *M. australe* C. Moore (in Moore and Betche, 1893: 208).

Holotype:—*Rudatis 149* (B, destroyed). Isotype:—**SOUTH AFRICA. KwaZulu-Natal**: Natal-Colony, district Alexandra, station Dumisa, farm Fairfield, elevation 750 m, 15 Nov. 1905, *Rudatis 149* (P! [P00412638]) (Fig. 6.2).

Evergreen understory shrubs and small trees 2–4 (–15) m; bark brownish grey, longitudinally furrowed; young branchlets slender, subquadrangular, older branchlets terete, whitish grey, longitudinally fissured; nodes thickened, internodes between normal leafy nodes (15–) 20–40 (–45) mm. Leaves thinly coriaceous, dark yellow to green and glossy above, paler green (yellow green) below; petioles 0.5–4 mm; leaf-blades broadly elliptic ovate to elliptic, (14–) 20–45 (–50) × (15–) 20–35 mm; base cuneate 15–30 (–35) mm wide; apex acutely acuminate, acumen 1–5 (–10) mm; mid-nerve clearly visible, impressed on the upper surface, ± prominent on the lower (especially toward leaf base); one pair of lateral nerves faintly visible on both surfaces, transverse veins obscure. Cymes ca. 4–6 (–10) mm, 1–3-flowered, mostly axillary or positioned mostly below the leaves at nodes having fully developed leaves, also at the intervening "aphyllous" nodes; peduncles 1–4 mm; secondary axes mostly 4–7 mm, bracts rapidly deciduous; bud biconical, 1–3 × 1–2 mm, corolla in bud rounded to subacute 3–4 mm. Flowers borne individually at the ends of the inflorescence axes, on pedicels 1–3 mm; hypantho-calyx green, obconic 3–4 (–7) × 2–3 (–5) mm; 4-lobed broadly rounded to triangular, green or suffused with dark purple 0.5–1 × 1–2 mm; petals white, broadly ovate to suborbicular, 2–5 × 2–4 mm, subacute at apex; staminal filaments 4–7 mm; anthers dolabriform, 1–2 × 1–2 mm, connective white with thecae positioned at anterior end, strongly incurved by dorsal oil-gland; anthers in bud rest on top of ovary and the epigynous chamber lacks partitions; style filiform, 5–10 mm. Fruits baccate, green, ellipsoid 3–6 (–8) × 2–5 (–7) mm, calycinal crown persistent 2 × 2 mm; 4-lobed, erect, broadly subacute to spreading 0.5–1 × 1 mm, fruit epigynous chamber marked only by scars of deciduous petals, anthers and style, with a shallow ridge (centre of ridge marked by deciduous style scar) radiating from the sides to centre; fruit pedicel 0.5–5 mm.

Additional specimens examined:—**SOUTH AFRICA. KwaZulu-Natal province**: Westville, 02 November 1893, *Medley-Wood 5232* (NH!, K!); South Coast, 15 July 1923, *I. B. P. E. 786* (K!); South Coast Natal, 15 July 1923, *Pole-Evans s.n* (PRE!); Zululand, Ngome Forest, Ngotshe District, 08 May 1944, *Gerstner 4497* (PRE!); Vryheid, elevation 3.600' m, 10 February 1952, *Edwards 2711* (PRE!); Ngoye Forest, Eshowe District, elevation 1300 ft., 16 February 1961, *Edwards 2488* (NU, PRE); Mtunzini, 16 February 1961, *Wells & Edwards 15* (NH!, NU!, PRE!); Ngome Forest, elevation 3600 ft., 10 February 1962, *Edwards 2715* (K!); Nature Reserve, elevation 1000′, 16 February 1966, *Moll 3025* (K!, PRE!); Pinetown, elevation 1.500 ft., 16 August 1966, *Moll 3297* (PRE!); Pine town, elevation 1.500 ft., 17 August 1966, *Moll 3305* (PRE!); Umzinto District, Umdoni Park, 15 April 1968, *Cooper 42* (NH!, PRE!); Nkandla, Ngoye Forest, (2831 DC), 11 December 1968, *Ross 1867* (NH!, PRE!); Kloof, cult. in Mr. Butcher's garden from seed collected above krantzes in Kloof Nature Reserve, December 1968, *Bayer 6285* (NH!, PRE!); Nkandla, Ngoye Forest, South fringe, (2831 DC), elevation 1.000' m, 11 December 1968, *Codd 10719* (PRE!); Mr. Butcher's garden, Wyebank, plant grown from seed collected at Krantzkloof Nature Reserve, 23 January 1969, *Ross 1890* (NH!, PRE!); Pietermaritzburg, Krantzkloof Nature Reserve, 23 January 1969, *Ross 1891* (NH!); Krantzfloof Nature Reserve, Understory tree 10ft high growing in deeper shade, (2930 DD), 23 January 1969, *Ross 1893* (NH!, PRE!); Kloof, in Mr R.R. Butcher's garden, 03 March 1969, *Bayer 6285a* (PRE!); Umdoni Park, 30 March 1969, *Jarman & Guy 193* (NU!); Port Shepstone, Ngongongo kloof forest bush, 30 March 1969, *Strey 8453* (NH!); Nkandla, Ngoye Forest, (2831 DC), 02 August 1969, *Ross 2120* (NH!, PRE!); Ngoye Forest, 01 November 1969, *Garland 453* (PRE!); Nkandla, Ngoye Forest, 23 November 1969, *Garland s.n.* (PRE!); Kloof Nature Reserve, elevation 1800′, 08 January 1970, *Bayer 6827* (NH!, PRE!); Oribi Nature Reserve, July 1970, *Moll 5025* (NH!, PRE!); Port Shepstone, Oribi Nature Reserve, forest near Hoopoo Falls. (3030 CB), July 1970, *Moll 5041* (NH!, PRE!); Ngoye Forest, 05 March 1972, *Moll 5625* (K!, NH!; PRE!); Ngoye Forest, elevation 1000′, 04 June 1972, *Moll & Müller 5672* (NH!, PRE!); Port Shepstone, Umdoni Park, (3030 BC), 10 December 1975, *Van Wyk & Venter 1376* (PRU!); Lusikisiki, Magwa, (3129 BC), 10 December 1975, *Van Wyk & Venter* 1349 (PRU!); Mtunzini, December 1975, *Garland s.n.* (K!); Oribi Gorge, along view point walk, 02 June 1978, *Van Wyk 2339* (PRU!); Farm "The Rocks" near Oribi Gorge, under canopy tree in forest along cliffs, 300 m, 10 October 1978, *Nicholson 1878* (NU!); "The Rocks", Izingolweni, 13 December 1978, *Nicholson 1910* (PRE!); Oribi Gorge Nature Reserve, Hell's Gate Gorge, 12 January 1979, *Nicholson 1918* (PRE!); Port Shepstone, 15 February 1979, (3030 CA), *Van Wyk 2627* (K!, PRU!); Uvongo, Ngongongo Kloof, naby pad na Gamalakhe, 11 December 1979, *Van Wyk 3288* (PRE!); Umtamvuna Nature Reserve, Gogosa Kloof, 06 October 1984, *Abbott 2175* (NH); Ngoye Forest, 12 October 1984, *Lowrey & Van Wyk 1043* (NH!, PRU!); Zululand, Ngoye Forest, 11 October 1984, *Lowrey & Van Wyk 1020* (PRU!); Ngome-Staatbos, Ntendeka Wilderness Area Woudrand, 04 December 1985, *Van Wyk 6985* (PRE!); Nkandla Forest Reserve, 03 April 1986, *Van Wyk 7332* (PRU!); Nqutu Falls, Krantzkloof, riverine forest, 17 September 1987, *Jordaan 1168* (NH!); Krantzkloof Nature Reserve, Nqutu Kloof, 17 September 1987, *Van Wyk 8117* (NH!, PRU!); Inanda District, Matabetule

Plateau, Mzinyati Nature Reserve, 18 September 1987, *Van Wyk 8159* (NH!, PRU!); Umhlatuzana River, Stainbank Nature Reserve, 28°52′30″S 31°37′30″E, 18 November 1994, *Nichols s.n.* (NH!); Thuthwini District, Ntimbankulu/Dweshula Village, near foot path to Mabheleni, through Ntimbankulu Forest, 30°37′30″S 30°22′30″E, 24 May 2001, *Ngwenya 2327* (NH!); KNR Durban, 16 February 2003, *Styles 1584* (NU!); Ngome, at campsite, Ntendeka Wilderness Area, (2731 CD), 11 June 2006, *Burrows & Burrows 9466* (BNRH!); Port Shepstone, Oribi Lake Eland Game reserve, 16 November 2006, Abbott 8546 (PRU!); Lake Eland Game Reserve, along foot path near suspension bridge below north rim of Oribi Gorge, elevation 587 m, 30°43′12.4″S, 30°11′14.5″E, 23 January 2009, *Stone et al. 2690* (NU!); Kenneth Stainbank Nature Reserve, Durban, along Red trail just where it meets south bank of the Umhlatuzana River, elevation 63 m, 29°54′10″S 30°56′19″E, 4 July 2013, *Stone & Cassimjee 2764* (NU!); Kenneth Stainbank Nature Reserve, Durban, along Red trail just below Idube picnic sites, elevation 57 m, 29°54′21″S, 30°56′45″E, 4 July 2013, *Stone & Cassimjee 2765* (NU!); Krantzkloof Nature Reserve, northern edge of Molweni gorge near lower Bridle Road viewpoint, elevation 460 m, 29°46′12″S, 30°50′10″E, upper reach of east-draining tributary ravine on Natal Group sandstone, 5 July 2013, *Stone et al. 2767* (NU!); Ngome State Forest, right-hand side of unpaved road below designated camping site, elevation 1130 m, 27°49′27″S 31°25′17″E, 8 July 2013, *Stone et al. 2768* (NU!); Ngome State Forest, along Forest Walk (foot path) to Cetshwayo's Refuge, elevation 1100 m, 27°49′48″S, 31°25′19″E, 8 July 2013, *Stone et al., 2770* (NU!); Ngome State Forest, along Forest Walk (foot path) to Cetshwayo's Refuge, elevation 1135 m, 27°49′37″S 31°25′08″E, 9 July 2013, *Stone et al. 2769,* (NU!); ~26.2 km straight-line distance west-southwest of Umzinto in Vulamehlo local municipality; near Moyeni Farm on escarpment overlooking the Mtwalume River (TOPOTYPE), elevation 725 m, 30°20'13''S, 30°23'26''E, 12 July 2013, *Stone et al. 2771* (NU!); ~25 km straight-line distance northwest and inland of KwaDukuza (Stanger), Mapumulo escarpment south of the Tugela River, elevation 792 m, 29°11′15.2″S 31°06′30.0″E, 25 October 2014, *Styles 4877* (NU!); Ongoye forest ca. 15 km inland from Mtunzini, elevation 350 m, 28°49′47.9″S 31°44′25.8″E, 17 July 2015, *Stone et al. 2788* (NU! 2 Sheets); Ongoye forest ca. 15 km inland from Mtunzini, elevation 375 m, 28°82′70.0″S 31°74′31.0″E, 17 July 2015, *Stone et al. 2789* (NU! 2 Sheets); Ongoye Forest ca. 15 km inland from Mtunzini, elevation 375 m, -28.82711°S, 31.74299°E, 07 December 2016, *Stone et al.*

2793 & *2794* (NU!). **Eastern Cape province:** East Pondoland, Egossa, August 1899, *Sim 2473* (PRE!); Cape, Lusikisiki, 08 September 1956, *Marais 1182* (PRE!); Port Edward, Umtamvuna, Hlolweni south bends, 25 April 1985, *Abbott 2589* (NH!, PRU!); Transkei, St. Johns, Mbotyi-Ntsubane Forest, (3125 BC), elevation 300 m, 24 May 1986, *Abbott 3147* (NH!; PRU!); Lusikisiki District, Lupatana, 10 December 1986, *Van Wyk & Mathews 7935* (NH!, PRU!); Lusikisiki District, Ntsubane - Mbotyi road just above the hairpin bend along lower part of steep-gradient, paved section, -31.44119°S, 29.73096°E, elevation ca. 225 m, 15 December 2016, *Stone 2803* (NU!). **Mpumalanga province:** Bearded Man, Songimvelo Nature Reserve, Barberton Mountains, elevation 1400 m, 16 April 2005, *Burrows & Lotter 8936* (BNRH!); Barberton Mountains, Bearded Man, Songimvelo Nature Reserve, on border of Swaziland above Satico gum tree plantation, elevation 1303 m, 25°44’44”S, 31°18’45”E, 26 September 2013, *Burrows et al. 13720* (BNRH); Barberton Mountains, Bearded Man, Songimvelo Nature Reserve, on border of Swaziland above Satico gum tree plantation, in deep shade of evergreen Afrotemperate forest (cloud forest), elevation 1299 m, 25°44’45”S, 31°18’45”E, 26 September 2013, *Burrows et al. 13721* (BNRH!); Barberton Mountains, Bearded Man, Songimvelo Nature Reserve, on border of Swaziland above Satico gum tree plantation, in deep shade of evergreen Afrotemperate forest (cloud forest), S-facing slope of mountain summit, elevation 1299 m, 25°44’44”S, 31°18’45”E, 26 September 2013, *Burrows et al. 13722* (BNRH); Barberton Mountains, Bearded Man, Songimvelo Nature Reserve, on border of Swaziland above Satico gum tree plantation, in deep shade of evergreen Afrotemperate forest (cloud forest), S-facing slope of mountain summit, elevation 1279 m, 25°44’50”S, 31°18’38”E, 26 September 2013, *Burrows et al. 13723* (BNRH). **Limpopo province:** Wolkberg Wilderness Area, Wolkberg farm 634 LT, occasional at waterfall, 23 October 1985, *Venter 11081* (NU!); Wolkberg Wilderness Area, Wolkberg farm 634 LT, occasional in Wonderwoud, 23 October 1985, *Venter 11149* (NU!)

Distribution and habitat:— The species is known from 19 locations including; fourteen in KwaZulu-Natal, three in Eastern Cape, one in Mpumalanga (Barberton Mts) and one in Limpopo (Wolkberg). It is found in coastal and mistbelt forests at elevations of ca. 60–1300 m. In the Wolkberg, the trees occupy higher elevations (ca.1760 m) in a forest classified as “afromontane” (Geldenhuys and Pieterse, 1993). (Fig. 6.1.).

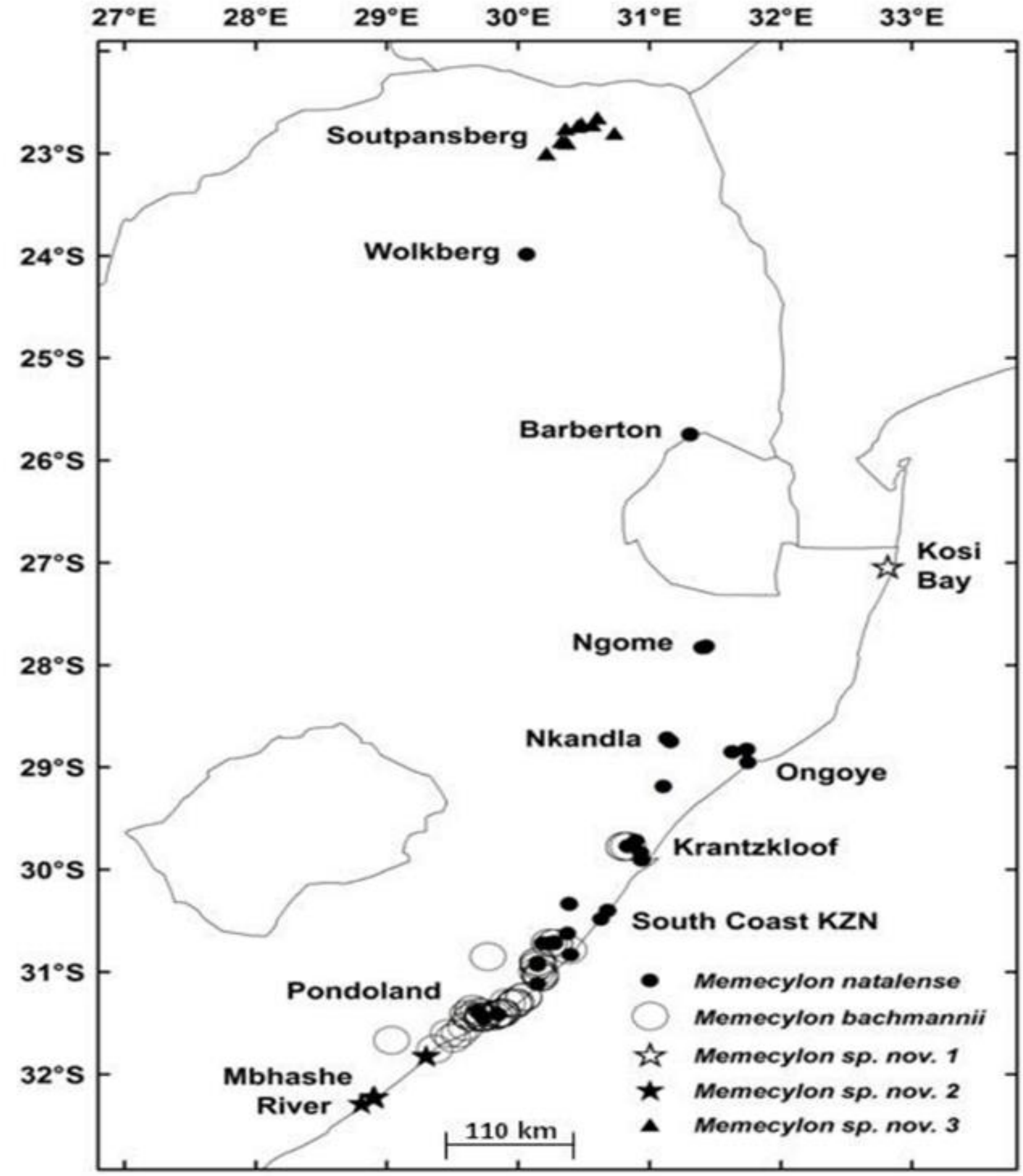


Figure 6.1. Distribution map of South African *Memecylon* species

Phenology:—Flowering recorded from early October to mid-December; immature fruits in early January to early June.

Conservation status:—*Memecylon natalense* has an EOO of ca. 99 683 km^2 and an AOO of ca. 104 km^2 (assuming a 4 km^2 grid-cell size). This species has not been assessed by SANBI because their Threatened Species Programme is currently systematically completing full assessments for all taxa with an automated status. Hence it was given an automated status of “Least Concern” (Foden and Potter, 2005). *Memecylon natalense* occurs mostly in protected conservation areas managed by Ezemvelo KZN Wildlife: Umtamvuna Nature Reserve, Oribi Gorge Nature Reserve, Kenneth Stainbank Nature Reserve, Krantzkloof Nature Reserve, and Nkandla Forest Reserve and Ongoye Forest. There are no documented significant threats in most of the conservation areas mentioned above.

The Ongoye Forest Nature Reserve is situated in the Ongoye range of hills, with the Mzimela community neighbours on all sides of the Reserve (Ezemvelo KZN Wildlife, 2009). The increase in homestead developments along the Ongoye Forest’s boundary within the Mzimela Traditional Authority has implications pertaining to access and management of the Forest (Krüger and Lawes, 2007). There is little control over casual exploitation in the forest such as: grazing of cattle on the grassland, trees being ring-barked for medicinal purposes and collection of firewood. The primary concern is that this harvesting targets pole-sized stems from mostly tree species that are confined to the forest understory (Boudreau et al., 2005). Another problem is the high fire frequency experienced annually that threatens the rich biodiversity of the forest (Krüger and Lawes, 2007).

At Nkandla Forest, the only previous collection of *M. natalense* was in April 1986 (*Van Wyk 7332*, PRU). The small trees were reportedly “rare”. The forest is threatened by habitat destruction as a result of forestry and overgrazing (von Staden and Abbott, 2007). Both Ongoye and Nkandla forest are assessed to be highly threatened because of their socio-economic importance (Goodman, 2000).

The *M. natalense* population in Umdoni Forest was not found during a visit in 2014 or during a follow-up visit in 2016. There are three previous collections from this forest, of which the most recent is from December 1975 (*Van Wyk & Venter 1376*, PRU). The forest appears to be degraded. Given that recent attempts to re-locate *M. natalense* at Umdoni Park have ended in failure, the species is likely extirpated at this site (pers. obs.).

In Eastern Cape province, the small-leaved *M. natalense* was collected at Mpahlane River in Mzamba, Lupatana (Luphuthana) river and the Ntsubane–Mbotyi road, these forests are not protected. The inaccessibility of the ravines and river gorges would make it extremely difficult for the locals to harvest wood, and the population is also not affected by frequent and intense grassland fires. Hence, the forests are relatively safe from the main threats affecting most Pondoland forests (von Staden and Abbott, 2007).

There is a population at Ngome State Forest, near the western extremities of Zululand, 70 km east of Vryheid. Other collections are from informal protected areas along roads (Ntsubane-Mbotyi; Ntimbankulu/Dweshula Village). There is a collection Stone *et al. 2771* that was made 26.2 km straight-line distance west-southwest of Umzinto in the Vulamehlo local municipality, near Moyeni farm on the escarpment overlooking the Mtwalume River

Songimvelo Nature Reserve (SNR), was a farmland before being proclaimed a protected area. Although people were removed from the area to create the reserve, some people and cattle have remained and continue to live inside its boundaries (Mpumalanga Tourism and Parks Agency [(MTPA]), 2014). The biggest threats to the reserve are the heavy overstocking of cattle (Steyn, 2003). Other threats include: annual burning of grass, invasive alien plants (blue gums [*Eucalyptus* species] and pines [*Pinus* species]) (MTPA, 2014), the harvesting of thatching grass, illegal settlements (homesteads) and illegal use of natural by the impoverished rural communities living alongside the Reserve (Stalmans et al., 1999).

Other collections (Venter 11081 & 11149, NU) are from the Wolkberg Wilderness Area. Threats here are not known or documented. Eight of the 19 known locations of *M. natalense* are found within formally protected areas. A status of “Least Concern”, is proposed with the caveat that this status is tentative based on the continued effectiveness of conservation measures within these protected areas.

Diagnostic features: *Memecylon natalense* is distinguished from the other South African *Memecylon* species by its broadly elliptic-ovate to elliptic leaf blades; cymes ca. 4–6 (–10) mm; peduncles 1–4 mm long; and calyx-lobes sometimes suffused with dark purple (Table 6.1.).

The *M. natalense* trees from Wolkberg Wilderness Area in Limpopo are morphologically unusual and ecologically distinct. They do not fit well within the circumscription of *M. natalense*. The leaves are very small and elliptic rather than being broadly elliptic ovate shape as reocorded in most *M. natalense* leaves.

Additional Note: A lectotype should be designated for M. natalense, because the holotype is lost”

The reason the P (From Peris Herbarium) specimen is not designated here as the Lectotype is because we want to avoid the possibility that this action would be considered valid under the rules of botanical nomenclature (Turland et al., 2018). Instead this action should be properly published in a journal article. For this dissertation, it is enough to say that the holotype in B is destroyed and an isotype has been located in P.

Figure 6.2. Isotype of *Memecylon natalense* (*Rudatis 149*, P). (Photo downloaded from https://science.mnhn.fr/institution/mnhn/collection/p/item/p00412638)

6.2.2. *Memecylon bachmannii* Engler

Memecylon bachmannii Engler (1921: 768).

Holotype:—not specified (B, destroyed). Neotype (designated by Van Wyk, 1983: 173).—**SOUTH AFRICA. KwaZulu-Natal:** Port Edward, Beacon Hill, woudrand, 08 January 1982, *Van Wyk 5318* (PRU! [PRU0047254-1]; isoneotypes K!, NH!, NU!, PRE!, PRU! [PRU0047254-2, PRU0047254-3]). (Fig. 6.4).

Heterotypic synonym:—*Memecylon grandiflorum* A. Fernandes & R. Fernandes (1955: 63, *tab. XVII*). Type:—**SOUTH AFRICA. Eastern Cape**: Lusikisiki District, Egosa Forest, in deep shade, 02 February 1929, *Galpin 9568* (holo- PRE!, iso- K!). (Fig. 6.4).

Evergreen understory to subcanopy shrub or small tree 3–4.5 m; bark brownish grey, longitudinally fissured; young branchlets slender, quadrangular to narrowly quadrangular-alate, emerging branchlets bronze to shiny dark purple; older branchlets terete, whitish grey, longitudinally fissured; nodes thickened; internodes between normal leafy nodes (25–) 40–85 (–100) mm. Leaves subcoriaceous, dark green and glossy above, pale green below; petioles light green to yellowish green, 0.5–2 mm, Leaf-blades broadly ovate and ± suborbicular (35–) 54–85 (–100) × (37–) 40–75 (–90) mm; rounded and ± shallowly cordate at base and confluent with petiole, 20–45 (–53) mm wide; abruptly acuminate at apex, acumen 2–4 (–6) mm; midnerve clearly visible, impressed on upper surface, ± prominent on lower surface (especially toward leaf base); one pair of lateral nerves faintly visible on both surfaces; transverse veins faintly visible 4–5 pairs, oblique relative to midnerve, ± prominent on both upper and lower surfaces, petiole 0.5–1 mm; floral buds biconical, 3–6 × 2–4 mm; corolla in bud rounded 3–7 mm; cymes 4–10 (–11) mm, 1–3(–5)-flowered, solitary or in fascicles of 2 at defoliated nodes of older branchlets, less often in the leaf axils; peduncle compressed, apex dilated, 0.5–2 mm; secondary axes mostly 3–5 mm. Flowers borne individually at ends of the inflorescence axes, on pedicels 0.5–1 mm; hypantho-calyx green, broadly cupuliform, 4–5 × 3–5 mm; calyx-lobes broadly subtriangular, 1–2 (–3) × 1–2 (–3) mm; 3 pairs of opposite-decussate bracteoles, persistent and clasping base of the hypantho-calyx; lower pair of bracteoles keeled on the back (1–) 3 × 1–3 mm, apex acuminate; middle pair of bracteoles broadly ovate-cordiform also dorsally carinate 2–4 × 2 (–4) mm, apex acuminate; upper pair of bracteoles concave 3–5 × 2–5 mm, apex acuminate; petals white, broadly ovate to subrhomboid, 3–7 × 2–5 mm, acuminate at apex; staminal filament 3–10 mm; anthers dolabriform, 1–2 × 1–2 mm, connective with thecae positioned at anterior end, strongly incurved by dorsal oil-gland, anther connectives white; style 5–12 mm; epigynous chamber with membranous partitions forming a V-shaped structure beneath each petal and sides of the chamber marked by staminal filament, a low, non-membranous ridge radiating from base of the style towards each episepalous stamen. Immature fruits baccate, green, ovoid, 4–10 (–14) × 4–6 (–10) mm, crowned by persistent calyx 2–5 × 1–3 mm, lobes erect, yellowish green, broadly rounded to subtriangular, 1–3 × 1–2 mm; fruit pedicel 0.5–2 mm.

Additional specimens examined:—SOUTH AFRICA. **KwaZulu-Natal province**: Port Shepstone District, Beacon Hill, ravine forest, 02 April 1966, *Strey 6502* (NH!, NU!, PRE!, UDW!); Port Shepstone District, Holgate’s Farm, Paddock, kloof forest, 6 August 1965, *Strey 5888* (NH!, NU!, PRE!, UDW!); Pietermaritzburg: Pinetown District., Everton, Eskotene, Molweni Kloof, 11 January 1970, *Hilliard 4898* (NH!, NU!); Umtamvuna Nature Reserve, near Port Edward, 01 July 1974, *Nicholson 1462* (PRE!); Port Edward, Beacon Hill, 23 February 1980, *Van Wyk 3628* (PRU!); Port Shepstone District, (3030 CC), against krans face in forest, 18 March 1982, *Abbott 49* (PRU!); Umtamvuna Nature Reserve, Bulolo north of office, 29 April 1984, *Abbott 1947* (NH!, PRU!); Umtamvuna River Gorge, under tall cliff forest on slopes above gorge, 20 December 1984, *Nicholson 2420* (NH!); Umtamvuna, radio beacon, forest, (3030 CC), 25 January 1985, *Abbott 2490* (PRU!);Umtamvuna Nature Reserve, Smedmore Forest adjoining reserve, 04 September 1994, *Van Wyk BSA 2577* (NH!, PRU!); Umtamvuna Nature Reserve, Umtamvuna gorge along Fish Eagle trail below Clearwater rest house, 31°02′53.8″S, 30°09′44.9″E, elevation 128 m, 21 January 2009, *Stone & Potgieter 2688* (NU!); Umtamvuna Nature Reserve, Umtavuna gorge along Fish Eagle trail below Clearwater rest house, elevation 142 m 31°02’41.5’’S, 30°09’58.3’’E., 21 January 2009, *Stone et al. 2689* (NU!); Everton, upper Molweni River drainage just above where crossed by Acutts Drive, elevation 550 m, 29°46’34’’S, 30°48’18’’E, 5 July 2013, *Stone et al. 2766 & 2766a* (NU!)

Eastern Cape province: Ngqeleni, November 1923, Miller in Herb. *Forestry 5439* (NU!); Transkei, Lusikisiki District, Magwa Falls, forest margin on banks of watercourse, elevation 1300 ft., 14 July 1966, *Ward 5792* (NH!, NU!, PRE!, UDW!); Transkei, Lusikisiki District, Magwa Falls, river[ine] forest, 14 July 1966, *Strey 6723*

(NH!, PRE!); Port Edward, near Beacon Hill Farm, in forest on steep North bank of Umtamvuna River, 10 December 1968, *Codd 10714* (NH!, PRE!); Cape, Port St. Johns, (3129 BD), 22 May 1970, *Jenkins s.n.* (PRE!); Kaap, Ntsubane, (3129 BC), 11 July 1976, *Venter 877* (PRE!); Mtentu River Gorge, 2 km upstream from mouth, 10 December 1978, *Cooper 257* (K!, PRE!); Port St. Johns, Ntsubane Fraser's Gorge, (3129 BC), 9 October 1982, *Van Wyk & Kok 5868* (PRU!); Transkei, Port Shepstone, Ntsubane, Fraser's Gorge, 09 October 1982, *Van Wyk & Kok 5866* (PRU!); Transkei, Port St. Johns, Ntsubane-Mbotyi, (3129 BC), 09 October 1982, *Van Wyk & Kok 5874* (PRU!); Lusikisiki District, Mlambomkulu River just where it exits from the Isicezula Forest, 04 December 1986, Isicezula Forest, bordering Mazizi Tea Estate, along main southern tributary of Mlambomkulu River, 08 December 1986, *Van Wyk & Matthews 7851* (NH!, PRU!); *Van Wyk & Matthews 7724* (NH!, PRU!); Umtentu River, north banks ±1 km inland, outside reserve, 10 December 1986, *Jordaan 964* (NH!, PRE!); Port St. Johns, Lusikisiki district, Mkeni river 1.5 km upstream from the sea, (3129 BD), 09 December 1986, *Van Wyk & Matthews 7883* (NH!, PRU!); Port St. Johns, Ntafufu Mtambalala Forest Station, 12 December 1986, *Van Wyk & Matthews 7975* (NH!, PRU!); Mkambati Nature Reserve, Daza River, 13 December 1986, *Jordaan 1071* (NH!, PRE!); Port St. Johns, Mount Sullivan, 12 April 1990, *Van Wyk 10051* (PRU!); Transkei, upper Bulawa Forest near Mpande, 22 June 1990, *Cooper 261* (NH!, PRE!); Transkei, Hlolweni River Gorge, confluence of Mtunzaana and Umtamvuna rivers, 30.999°S 30.140°E, elevation 369 m, 13 December 1993, *Van Wyk BSA 1601* (PRU!); Transkei, Mzamba, Hlolweni River at junction with Icwaka, elevation 250 m, 15 December 1994, *Abbott 6635* (PRU!); Port Edward, Umtamvuna, (3130 AA), 23 March 2010, *Abbott 9150* (BNRH!); Lusikisiki District, Magwa Falls, right bank of Mzizangwa River ca. 100 m upstream of falls, 31°26′41.8″S 20°38′26.9″E, 10 June 2015, *Stone & Tenza 2781* (NU!);Lusikisiki District, Magwa Falls, right bank of Mzizangwa River just upstream of falls, 31°26′38.9″S, 29°38′24.6″E, elevation 400 m, 10 June 2015, *Stone & Tenza 2782* (NU!); Port St. Johns district, Silaka Nature Reserve, in rocky ground on right bank of Gxwaleni River, densely shaded forest understory, elevation 50 m, 31°38′56.7″S, 29°30′01.6″E, 12 June 2015, *Stone 2785* (NU!); Lusikisiki District, Ntsubane–Mbotyi road just above the hairpin bend along lower part of steep-gradient, paved section, -31.44119°S, 29.73096°E, elevation ca. 225 m, 15 December 2016, *Stone et al. 2804* (NU!); Lusikisiki District, Ntsubane – Mbotyi road above the steep-gradient, paved section, elevation 390 m, -31.42820°S, 29.72638°E, 15 December 2016, *Stone et al. 2805* (NU!).

Distribution and habitat:—*Memecylon bachmannii* is known from ca. 18 locations including three or four in southern KwaZulu-Natal and 14 from Pondoland in the adjacent Eastern Cape (Fig. 6.1.). The habitat is in shaded understory of coastal evergreen forest, on weathered sandstone soil at elevations of 25–550 m (R.D. Stone, pers. obs., 11 December 2017).

Phenology:— Flowering recorded in early December to mid-February; immature fruits in late December to early March.

Conservation status:— *Memecylon bachmannii* was previously assessed as “Least Concern” in the Red List of South African Plants (von Staden and Abbott, 2007). It has an EOO of ca. 8 751 km^2 and an AOO of ca. 120 km^2 (assuming a 4 km^2 grid-cell size). The species occurs in the coastal region of southern KwaZulu-Natal and the adjacent Eastern Cape. There are isolated occurrences northwards near Durban and southwards in the region of Port St Johns.

The Mkambati Nature Reserve is located at the coast of north-eastern Pondoland, in the Eastern Cape. Few threats are reported in Mkambati Nature Reserve, these include frequent fires (Hamer and Slotow, 2017) and the opening of the controversial cast dune mine (Dippenaar-Schoeman et al., 2011; Hamer and Slotow, 2017). This affects the soil composition of the forests and consequently floral diversity (Dippenaar-Schoeman et al., 2011). Invasive alien plants are also troublesome in the forest, e.g., trifid weed (*Chromolaena odorata* (L.) R.M. King & H. Rob. black wattle (*Acacia mearnsii* De Wild.), tickberry (*Lantana camara* L.) and guava (*Psidium* L. species) (Dippenaar-Schoeman et al., 2011).

The Ntsubane Forest complex is located in the northern part of Pondoland in the Eastern Cape province. It is the largest remaining indigenous forest complex on the Wild Coast, also identified as a Key Biodiversity Area within the Maputaland–Pondoland–Albany Hotspot (SANBI and Wildlands Conservation Trust, 2015). The area is made up of several increasingly fragmented Forest clusters (Mbotyi forest, Lupatana Nature Reserve, Egossa Forest). All the forest types in the area are threatened as they are not formally protected, except those with limited protection under the National Forest Act (84 of 1998) (SANBI and Wildlands Conservation Trust, 2015).

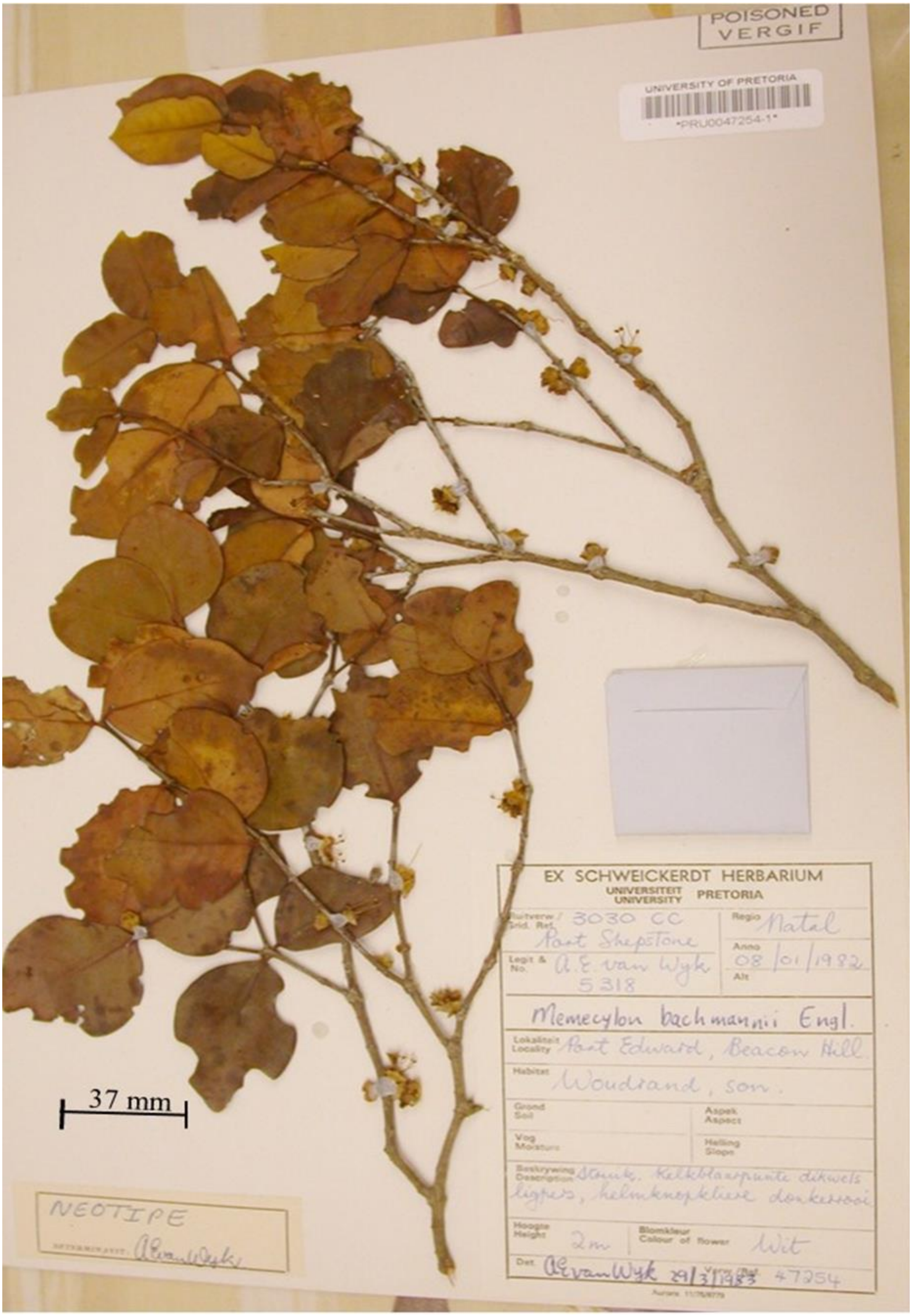
The site at Magwa Falls near Ntsubane is easily accessed, with suspected reduction of the *M. bachmannii* population caused by wood cutting and forest degradation. Threats in the Lupatana Nature Reserve and Egossa Forest are unknown.

In KwaZulu-Natal, the Umtamvuna Nature Reserve near Port Edward is well protected from habitat destruction, but a potential threat stems from excessive water extraction by gum plantations outside the reserve boundaries which negatively affects the moist seepage of the forest (Raimondo and von Staden, 2008). This may have a negative effect on the *M. bachmannii* population in the long term.

The forest in Eskotene Kloof near the Molweni River is potentially threatened by urban expansion (Victor, 2006). Seven of the 18 known locations of *M. bachmannii* are in formally protected areas, a status of “Least Concern” is thus proposed with the caveat that this status is tentative based on the continued effectiveness of conservation measures within these protected areas.

Diagnostic features: *Memecylon bachmannii* is clearly distinguished from *M. natalense* by its broadly ovate ± suborbicular blades, that are bigger (35–) 54–85 (–100) × (37–) 40–75 (–90) mm (versus elliptic and broadly elliptic ovate leaf blades, that are smaller [14–] 20–45 [–50] × [15–] 20–35 mm); wider rounded ± shallowly cordate base 20–45 (–53) mm (versus cuneate base that is less wider 15–30 [–35] mm); very short petiole 0.5–1 mm (versus slightly longer petioles [–0.5] 1–4 mm); flower buds are bigger 3–6 × 2–4 mm and corolla in buds are rounded and also bigger 3–7 mm (versus smaller flower buds 2–4 × 2–3 mm, corolla in buds are rounded to subacute and smaller 3–4 mm); larger flowers ca. 10 mm (versus smaller flowers ca. 5–7 mm); hypantho-calyx bigger 4–8 × 3–5 mm (versus smaller hypantho-calyx 3–4 [–7] × 2–3 [–5] mm); hypantho-calyx lobes broadly rounded to subtriangular and slightly bigger 1–2(–3) × 1–2 (–3) mm (versus hypantho-calyx lobes broadly rounded to triangular, green or suffused with dark purple and are smaller 0.5–1 × 1–2 mm); peduncle compressed 0.5–2 mm (versus peduncle not compressed 1–4 mm); fruit ovoid, and bigger 4–10 (–14) × 4–6 (–10) mm (versus fruit ellipsoid and smaller 3–6 [–8] × 2–5 [–7] mm); yellowish green broadly rounded to subtriangular fruit calycinal lobes 1–3 × 1–2 mm (versus fruit calycinal lobes broadly subacute to spreading sometimes suffused with dark purple 1×1 mm); and fruit pedicel shorter 0.5–2 mm (versus fruit pedicel longer 0.5–5 mm) (Table 6.1.).

M. bachmannii differs from *M.* sp. nov. 2 by its longer internodes between normal leafy nodes (25–) 40–85 (–100) mm (versus shorter internodes 25–35 [–50] mm); bigger leaf-blades broadly rounded ± suborbicular, (35–) 54–85 (–100) × (37–) 40–75 (–90) mm (versus broadly ovate leaf-blades that are smaller 35–45 [–55] × [25–] 30–35 [–40] mm); obtuse ± shallowly cordate wider base 20–45 (–53) mm (versus obtuse less wider base 14–30 mm); larger floral persistent bracteoles: lower pair of bracteoles (1–) 3 × 1–3 mm, middle pair of bracteoles 2–4 × 2 (–4) mm and upper pair of bracteoles 3–5 × 2.5 mm (versus smaller bracteoles: lower pair of bracteoles [0.5] 1 × 1.5 mm; middle pair of bracteoles 2 × 1.5 [–2] mm; upper pair of bracteoles 2 × 3 mm); bigger fruits 4–10 (–14) × 4–6 (–10) mm (versus smaller fruits 4–7 × 3–5 mm); crowned with bigger persistent calyx 2–5 × 1–3 mm (versus crowned with smaller persistent calyx 1 × 1–2 mm); fruit calyx lobes bigger 1–3 × 1–2 mm (versus fruit calyx lobes smaller 1 × 1 mm) (Table 6.1.).



EX SCHWEICKERDT HERBARIUM
UNIVERSITEIT UNIVERSITY PRETORIA

Ruitverw./Grid. Ref. 3030 CC Port Shepstone
Regio Natal
Legit & No. A.E. van Wyk 5318
Anno 08/01/1982
Alt

Memecylon bachmannii Engl.

Lokaliteit Locality Port Edward, Beacon Hill
Habitat Woudrand, son.
Grond Soil
Aspek Aspect
Vog Moisture
Helling Slope
Beskrywing Description Struik, kelkblaarpunte dikwels ligpers, helmknopklier donkerrooi
Hoogte Height 2m
Blomkleur Colour of flower Wit
Det. AEvanWyk 29/3/1983 47254

Determinavit: AEvanWyk

Figure 6.3. Neotype of *Memecylon bachmannii* (*Van Wyk 5318,* PRU).

Figure 6.4. Holotype of *Memecylon grandiflorum* (*Galpin 9568*, PRE).

(Photo by Lindelwa Khumalo)

6.2.3. *Memecylon* sp. nov. 1

SOUTH AFRICA. KwaZulu-Natal: Kosi Bay Nature Reserve, ca. 0.8 km southwest of where the Sihadla (Siyadla) River flows into Lake Amanzimnyama, elevation ca. 20 m, 27°02'14.14"S, 32°48'45.76"°E, 08 December 2016, *Stone & Mona 2795* (NU!, duplicates BNRH, K, NH, PRE) (Fig. 6.5).

Evergreen understory to subcanopy tree, 4–10 (–12) m; bark brownish grey, longitudinally fissured; young branchlets slender, quadrangular to narrowly quadrangular-alate; older branchlets terete, whitish grey, longitudinally fissured; nodes thickened; internodes between normal leafy nodes 20–30 (–60) mm. Leaves subcoriaceous, dark green and glossy above, somewhat paler below; petioles 1.5–3 mm; leaf-blades elliptic to obovate, (30–) 40–60 (–80) × (12–) 18–30 (–38) mm, cuneate at base (margins curved slightly inwards) and confluent with petiole, ± broadly and obtusely acuminate at apex, acumen (2–) 3–6 (–8) mm (sometimes indistinct or with apex acute); midnerve clearly visible, impressed on upper surface, ± prominent on lower (especially toward leaf base); one pair of lateral nerves faintly visible on both surfaces, course curvilinear and 1–3 mm from margin in basal half of blade; transverse veins 4–5 pairs, faintly visible, oblique relative to midnerve, ± prominent on both upper and lower surfaces in dried material. Cymes 1–3 (–5)-flowered, solitary or in fascicles of 2–3 at defoliated nodes of older branchlets, less often in leaf axils and at bracteolate nodes alternating with those bearing fully developed leaves, occasionally borne terminally; peduncles (0.5–) 3–5 (–6.5) mm; secondary axes 1–3 in number, mostly 2–3 mm, additional axes when present of similar dimensions; bracts rapidly deciduous. Flowers borne individually at ends of inflorescence axes, on pedicels 1–2 (–3) mm; hypantho-calyx green, obconic to cupulo-patellate, 3 × 4 mm, margin sinuate-dentate; lobes broadly rounded, each with scarious margin ca. ½ mm high, irregularly erose-denticulate (occasionally with one or more lobes incised to form larger teeth); corolla in bud rounded-apiculate; petals white, broadly ovate to suborbicular, 4 × 4–4.5 mm, shortly apiculate at apex; staminal filaments 4–6 mm; anthers dolabriform, 1–1.25 × 1.5–1.8 mm , connective yellow in colour with thecae positioned at anterior end, strongly incurved by the dorsal oil-gland; style 8×10 mm, epigynous chamber with membranous partitions forming a V-shaped structure beneath each petal and with a low, non-membranous ridge radiating from the base of style towards each episepalous stamen. Immature fruits green, subglobose, 7 – 8 mm in diameter, crowned by persistent calyx 1.5 × 3 mm, lobes rounded, scarious, erect; fruit pedicel 4–7 mm.

Additional specimens examined:—SOUTH AFRICA. KwaZulu-Natal: Kosi Bay Nature Reserve, Sihadla forest where Sihadla River flows into Lake Amanzimnyana, 01 December 2002, *Styles 1391* (NU!, 2 sheets); Kosi Bay Nature Reserve, 09 April 2011, *Styles 3539* (NH!); type loc., elevation 23 m, 27°02'12.5"S, 32°48'50.9"E, 07 February 2017, *Stone et al. 2806* (NU!, NH, PRE, BNRH); type loc., elevation 24 m, 27°02'12.2"S, 32°48'50.8"E, 07 February 2017, *Stone et al. 2807* (NU!, NH, PRE, BNRH).

Distribution and habitat:—Known only from the type locality in northeastern KwaZulu-Natal, South Africa (Fig. 6.1.). Habitat in high, mature, lowland forest on loamy sand, at about 20–25 m elevation. The full extent of the population is unknown, and more extensive field-work is needed inside the Kosi Bay Nature Reserve.

Phenology:— Flowering recorded in early December; immature fruits in early February.

Conservation status:—*Memecylon* sp. nov. 1 is known from a single location with an area of occupancy (AOO) of 4 km^2 (assuming a 4 km^2 grid cell size). The population occurs within a formally protected area, the Kosi Bay Nature Reserve, which is part of the larger iSimangaliso Wetland Park administered by the iSimangaliso Authority. Threats in the area are not well documented but may include limited use of forest resources by local people (e.g. selective removal of timber) and uncontrolled fires may affect the forest during extended periods of drought. Access to the forest is only possible by a 4×4 vehicle track or on foot, but there is evidence of increasing human population pressure outside the reserve, in the vicinity of the town of Manguzi (KwaNgwanase). Of more immediate concern is the evidently small size of the *Memecylon* population (± 50 individual trees) and its very limited AOO, such that a single event with a large impact (e.g. fire) could conceivably affect all of the known individuals. *Memecylon* sp. nov. 1 is thus provisionally assessed as “Vulnerable” [VU D2] according to the IUCN Red List Categories and Criteria (IUCN, 2012).

Diagnostic features: *Memecylon* sp. nov. 1 differs from *M. natalense* in having obovate leaf-blades (versus broadly ovate to broadly elliptic ovate leaf-blades), broadly and obtusely acuminate apex (versus acuminate to acute apex); fruit calycinal crown lobes that are rounded and have scarious teeth (versus fruit calycinal crown lobes subacute with no scarious teeth) (Table 6.1.).

M. sp. nov. 1 is closely related to the Mozambican *M. incisilobum,* as evidenced by the 100% nrDNA sequence identity between these two populations (Stone, 2014; Stone et al., 2017a). Both populations are found in the region of northeastern KwaZulu-Natal and southernmost Mozambique known as Maputaland (Van Wyk, 1996), but are separated from each other by an airline distance of ca. 200 km. However, there are several morphological differences between them.

M. sp. nov. 1 differs from *M. incisilobum* by having a cymes or flowers in fascicles of 2–3 (versus cymes solitary or rarely geminate); shorter inflorescence axes: peduncles mostly 3–5 mm (versus longer inflorescence axis; mm peduncle 5–10) and secondary axes mostly 2–3 mm (versus 3.5–7 mm secondary axes); less numerous flowers mostly 1–3, rarely 4 or 5 per cyme flowers (versus up to 9 flowers per cyme); hypantho-calyx differently shaped, obconic to cupulo-patellate (versus broadly cupuliform hypantho-calyx); scarious margin ca. 0.5 mm high and irregularly erose-denticulate or occasionally with one lobe shallowly incised (versus calyx-lobes with scarious margin ca. 1 mm and regularly incised ± to the base); shorter styles ca. 7 mm (versus longer style 8–10 mm); rounded-apiculate corolla in bud (versus corolla in bud sharply apiculate with apiculum ca. 1 mm high); and fruit with calycinal crown not thickened and collar-like, lobes erect (versus fruits with calycinal crown thickened and collar-like with lobes curved inwards) (Table 6.1.). There also seems to be a difference in their respective flowering times for these two taxa (late October for *M. incisilobum*, early December for the Kosi Bay *Memecylon* sp. nov. 1.).

SOUTH AFRICA

Memecylon sp. nov.

KwaZulu-Natal : Kosi Bay Nature Reserve, c. 0.8 km southwest of where the Sihadla [Siyadla] River flows into Lake Amanzimyana, GPS coordinates - 27.03726°S, 32.81271°E, elevation c. 20 m, in high, mature, lowland forest on loamy sand. Flowers white (photos & collection in 70% alcohol), collected from a 10-m tree that had fallen over (due to a fire caused by a lightning strike?). *Memecylon* is otherwise a locally frequent understorey/subcanopy tree in this forest, but no seedlings or saplings were seen, indicating that reproduction and/or seedling establishment are rare events. With Gracious Mona.

Stone R.D. 2795 08 December 2016

Figure 6.5. *Memecylon* sp. nov. 1 (*Stone & Mona 2795*, NU).

(Photo by Dr R.D. Stone)

6.2.4. *Memecylon* sp. nov. 2

SOUTH AFRICA. Eastern Cape, (3228 BB) (Butterworth): Gwibi (= Cwebe) Forest, near Bashee (= Mbhashe) River mouth, 25 November 1971, *Gordon-Gray* s.n. (NU!, duplicate PRE [accession no. 51136]).

Evergreen understory to subcanopy shrub or small tree, 2–4.5 m tall; bark brownish grey, longitudinally fissured; young branchlets slender, quadrangular to narrowly quadrangular-alate; older branchlets terete, whitish grey, longitudinally fissured; nodes thickened; internodes between normal leafy nodes 25–35 (–50) mm. Leaves subcoriaceous, dark green and glossy above, paler below; petioles 1–3 mm, blades broadly elliptic-ovate ± suborbicular , 35–45 (–55) × (25–) 30–35 (–40) mm; base 14–30 mm wide cuneate. ± rounded and confluent with the petiole; petiole 0.5–2 mm; apex acutely acuminate, acumen 3–4 (–5) mm; midnerve clearly visible, impressed on upper surface, ± prominent on lower (especially toward the leaf base); one pair of lateral nerves faintly visible on both surfaces; transverse veins faintly visible 4–5 pairs, oblique relative to the midnerve, ± prominent on both upper and lower surfaces in dried material. Cymes 1–3-flowered, solitary or in fascicles of 2–3 at defoliated nodes of older branchlets, less often in leaf axils and at the bracteolate nodes alternating with those bearing fully developed leaves; peduncle compressed, apex dilated, 1–2 (–3) mm; secondary axes mostly 2–4 mm; bracts rapidly deciduous. Flowers borne individually at the ends of inflorescence axes, on pedicels 1–2 (–3) mm; hypantho-calyx green, campanulate, 3 × 4 mm, lobes broadly rounded to subtriangular; 3 pairs of opposite-decussate bracteoles, persistent and clasping base of hypantho-calyx; lower pair of bracteoles keeled on the back, apex acuminate, (0.5–) 1 × 1.5 mm; middle pair of bracteoles broadly ovate-cordiform also dorsally carinate, apex acuminate 2 × 1.5 (–2) mm; upper pair of bracteoles concave, apex acuminate 2 × 3 mm; bud biconical, corolla in bud rounded-apiculate; petals white, broadly ovate to subrhomboid, 3 × 2 mm, apex acuminate; staminal filaments 8 mm; anthers dolabriform, 2 × 1 mm, the connective with thecae positioned at anterior end, strongly incurved by the dorsal oil-gland; style 8 mm; immature fruits baccate, green, ovoid, 4–7 × 3–5 mm, crowned by the persistent calyx 1 × 1–2 mm, 4-lobed, erect, broadly rounded to subtriangulular 1×1 mm, epigynous chamber marked by scars of the deciduous petals, anthers and style.

Additional specimens examined:—**SOUTH AFRICA. Eastern Cape province:** Bashee River mouth, in forest, (3228 BB), 27 May 1970, *Jenkins s.n.* (NU!, 2 sheets); Transkei Region, Elliotdale District, The Haven, in forest, 27 Feb. 1971, *Gordon-Gray 2005* (NU!, 2 sheets); Dweza Nature Reserve, near Willowvale, southern Transkei, forest near Shone Cottage. (3228 BD), 17 July 1985, *Cooper 290* (NH!); Dwesa Nature Reserve, (3228 BD), 10 August 1988, *Van Wyk 8299* (PRU!); Dwesa-Cwebe Nature Reserve, on north side of Mbashe River, elevation ± 100 m a.s.l., locality within 100 m of GPS position -32.22778S, 28.89570E, 31 December 2013, *Styles 4769* (NU! 2 sheets); Dwesa-Cwebe Nature Reserve, north side of the Mbashe River, elevation ± 100 m a.s.l., locality within 100 m of GPS position -32.22687S 28.89679E, 02 January 2014, *Styles 4770* (NU!). Dwesa-Cwebe Nature Reserve, on north side of Mbashe River, elevation ± 100 m a.s.l., locality within 100 m of GPS position -32.22610S, 28.89730E, 02 January 2014, *Styles 4771* (NU!); Hluleka Nature Reserve, along “Management Road” coastal forest understory 31°49’37.9’’S. 29°17’46.8’’E, elevation 45 m,. *Stone & Tenza 2783* (NU! 2 sheets); Hluleka Nature Reserve, along “Management Road” coastal forest understory, elevation 45 m, 31°49’05.2’’S. 29°18’02.5’’E, *Stone & Tenza 2784* (NU! 3 sheet); Dwesa-Cwebe Nature Reserve, along unpaved road leading from main gate towards the Haven Hotel, then after less than 1 km turn left onto unpaved road towards Gate 1 through dense coastal forest, elevation ca. 120 m, -32.22576°S, 28.906277°E, , 12 December 2016, *Stone & Mona 2800* (NU!); Dwesa-Cwebe Nature Reserve, approx. same locality, elevation ca. 150 m, -32.22371°S, 28.90647°E, 12 December 2016, *Stone et al. 2801* (NU!); Dwesa-Cwebe Nature Reserve, approximately same locality elevation ca. 135 m, -32.22246°S, 28.90707°E, 12 December 2016, *Stone et al. 2802* (NU!).

Distribution and habitat:—*Memecylon* sp. nov. 2 is currently known from three locations, the Dwesa Forest, Cwebe Forest and Hluleka Nature Reserve in Eastern Cape province, South Africa (Fig. 6.1.). The Dwesa and Cwebe are two parts that are separated by the Mbhashe River (one of the largest rivers in the former Transkei). The Dwesa part is on the south side of the river and the Cwebe part is on the north side (Timmermans, 2004). Most of the collections are from the northern (Cwebe) part, but there are two collections (*Cooper 290* [NH] and *Van Wyk 8299* [PRU]) that appear to be from the southern (Dwesa) part. The Cwebe coastal forest is located on the north side of the Mbashe River, on soils weathered from finely grained sandstones and mudstones, at an elevation of about 100-150 m. The trees are locally common in a dense forest along the unpaved road leading towards Gate 1.

The Hluleka Nature Reserve is located along the coast about 30 km south of Port St. Johns. Coastal and scarp forest covers approximately 70% of the reserve, whereas the remainder is made up of thicket and Transkei Coastal Belt Grassland (Mucina and Geldenhuys, 2006). *Memecylon* sp. nov. 2 was observed to be locally common in forest along the "Management Road" at elevations from near sea level to ca. 45 m.

Phenology:— Flowering recorded in late November; fruits in December to July.

Conservation status: *M*. sp. nov. 2 is known from three localities: Dwesa-Cwebe and Hluleka Nature Reserves are found in the Eastern Cape. It has an EOO of ca. 93 km^2 and an AOO of 12 km^2 (assuming a 4 km^2 grid cell size). The Dwesa-Cwebe Nature Reserve has an area of 42.5 km^2 (Palmer et al., 2002) and is formally protected; threats to these forests are therefore considered limited. The Hluleka Nature Reserve is also protected, and threats in this area are undocumented. Given that all of the known locations are in formally protected areas, and that the species is "locally common" in both the Hluleka and Cwebe forests, a status of "Least Concern" for *M.* sp. nov. 2 is proposed, with the caveat that this status is tentative based on the continued effectiveness of conservation measures within these protected areas.

Diagnostic features: *Memecylon* sp. nov. 2 shares certain character-states with *M. bachmannii* (suborbicular leaf-blades, rounded base, persistent floral bracteoles and ovoid fruit shape), but the results of the phenetic analysis (Chapter 3) indicate it has greater overall similarity to *M. natalense*.

M. sp. nov. 2 differs from *M. bachmannii* by its shorter internodes 25–35 (–50) mm (versus longer internodes between normal leafy nodes [25–] 40–85 [–100] mm); broadly ovate leaf-blades that are smaller 35–45 (–55) × (25–) 30–35 (–40) mm (versus bigger leaf-blades suborbicular ± rounded, [35–] 54–85 [–100] × [37–] 40–75 [–90] mm); less wider base 14–30 mm (versus wider base 20–45 [–53] mm); smaller bracteoles: lower pair of bracteoles (0.5) 1 × 1.5 mm; middle pair of bracteoles 2 × 1.5 (–2) mm; upper pair of bracteoles 2 × 3 mm; (versus larger floral persistent bracteoles: lower pair of bracteoles [1–] 3 × 1–3 mm, middle pair of bracteoles 2–4 × 2[–4] mm and upper pair of bracteoles 3–5 × 2.5 mm); a smaller fruits 4–7 × 3–5 mm (versus bigger fruits 4–10 [–14] × 4–6 [–10] mm); crowned with smaller persistent calyx 1 ×

1–2 mm high (versus crowned with bigger persistent calyx 2–5 × 1–3 mm); and fruit calyx lobes smaller 1×1 mm (versus fruit calyx lobes lobes bigger 1–3 × 1–2 mm) (Table 6.1.).

Memecylon sp. nov. 2 is distinguished from *M. natalense* by its broadly rounded leaf-blades (versus broadly elliptic ovate and elliptic leaf-blades); rounded base (versus cuneate base); persistent bracteoles that clasp at the bottom of the hypantho-calyx and fruit (versus bracts rapidly deciduous), rounded-apiculate corolla in bud (versus rounded to subacute corolla in bud); broadly ovate to subrhomboid, 3 × 2 mm petals (versus broadly ovate to suborbicular, 2–5 × 2–4 mm petals); ovoid fruit (versus ellipsoid fruit), fruit calycinal lobes are yellowish green broadly rounded to sub-triangulular (versus fruit calycinal lobes broadly subacute to spreading sometimes suffused with dark purple) (Table 6.1.**).**

NATIONAL NASIONALE HERBARIUM PRETORIA

3228BB (BUTTERWORTH)	Grid Ref./ Ruitverw.	Regio	CAPE
Col. JOHN L. GORDON GRAY	Legit & No.	Anno Ait.	25/11/1971

Memecylon grandiflorum R. & A. Fernandes

Gwibi Forest, near Bashee River Mouth.
Copy of letter from Col. John L. Gordon Gray attached.

Det. Ref./Verw.

GP-S-(F)-8 LTD 1506

UNIVERSITY OF NATAL HERBARIUM

5788/1

UNIVERSITY OF NATAL, HERBARIUM No

FAMILY

NAME Memecylon grandiflorum R&A Fernandes

LOCALITY Gwibi Forest, near Bashee River Mouth. 3228 BB (Butterworth) Cape

COLL. No. DATE 25/11/1971 ALT

COLL. Col. John L. Gordon Gray DET

TEEANEM 5442-2-84

POISONED

Figure 6.6. *Memecylon* sp. nov. 2 (*Gordon-Gray s.n.* on 25 Nov. 1971, NU).

(Photo by Dr R.D. Stone)

6.2.5. ***Memecylon* sp. nov. 3**

SOUTH AFRICA. Limpopo: Eastern Soutpansberg, ca. 5 km East of Tshumulungwi on road to Mufulwi, elevation 1124 m, 22.73055556°S, 30.45277778°E, 28 November 2013, *J. Burrows & S. Burrows 13905* (BNRH!, duplicates K, NU).

Evergreen understory to subcanopy shrubs and small trees, 2–3 (–5) m tall; bark brownish grey, longitudinally furrowed; young branchlets slender, subquadrangular, older branchlets terete, whitish grey, longitudinally fissured; nodes thickened; internodes between normal leafy nodes 18–40 (–54) mm. Leaves subcoriaceous, blades ovate to broadly ovate (25–) 30–45 (–55) × (18–) 20–35 mm; base obtuse or rounded; apex acutely acuminate, acumen (2–) 4–6 (–10) mm; leaves dark yellowish green and glossy above, paler below; midnerve clearly visible, impressed on the upper surface, ± prominent on the lower surface (especially toward the leaf base); one pair of lateral nerves faintly visible on both surfaces, lower surface transverse veins visible, petioles 0.5–2 mm. Cymes ca. 6–10 mm, 1–3-flowered, solitary or in fascicles of 2 at the defoliated nodes of older branchlets, at bracteolate nodes alternating with those bearing fully developed leaves; peduncles 5–8 (–10) mm; secondary axes mostly 5–10 mm, bracts rapidly deciduous. Flowers borne individually at the ends of the inflorescence axes, on pedicels 3–4 (–5) mm; hypantho-calyx green, obconic, 2–3 × 2–4 mm, calyx lobes broadly rounded to triangular, 1×1 mm; floral buds biconical 2–4 (–5) × 2–3 mm, acutely apiculate corolla in bud; flower petals white, broadly ovate to suborbicular, 2–4 × 2–3 mm, shortly apiculate at the apex; staminal filaments 5–9 mm; anthers dolabriform, 1–2 × 1–1.5 mm, the connective with thecae positioned at the anterior end, anther connectives white, strongly incurved by the dorsal oil-gland; style filiform, 6–10 mm, epigynous chamber the anthers in bud are resting on the top of the ovary and are often separated from each other my membranous partitions radiating outwards from the base of the style. Fruits baccate, green, ellipsoid 4–6 × 4–7 mm, calycinal crown persistent 1–2 mm; erect, to spreading, lobes broadly subacute; fruit pedicel (3–) 5–10 mm.

Additional specimens examined:—SOUTH AFRICA. Limpopo province: Entabeni Forest, January 1925, *Keel s.n.* (PRE!); Tate Vondo, Sibasa District along Tshirovha River, (2230 CD), 22°53’S, 30°22’E, 10 December 1977, *Hemm 420* (PRE!); Tate Vondo, elevation 1050 m, (2230 CB), 30 June 1978, *Hemm. s.n.* (K, MO, PRE!); Tate

Vondo, Mohovho-hovho Waterval, (2230 DC), 19 April 1979, *Van Wyk 2803* (PRE, PRU! 2 Sheets); Tate Vondo, Mohovho-hovho Waterval, (2230 DC), 20 April 1979, *Van Wyk 2852* (PRU!); Entabeni Staatbos, 13 June 1979, elevation 1300 m, *Von Breitenbach s.n.* (PRE!); Venda, next to dirt road between Thengwe and Tshixwadza, elevation 923 m, (2230 CB), 13 June 1979, *Van Wyk BSA 2019* (PRE!, PRU! 2 Sheets); Venda Region, Tate Vondo, Mahovhohovho waterfall, 6 February 1980, *Van Wyk 3634* (PRE!, PRU!); Soutpansberg, Messina, Mohovho-hovho Waterval, (2230 CD), 6 February 1980, *Van Rooyen s.n.* (PRU! 2 Sheets); Tshaulu, Mutanzhela, (2230 DC), 10 April 1980, *Van Wyk 3872* (PRU!); Thengwe, Vuvha, (2230 DA), 11 April 1980, *Van Wyk 3931* (PRU!); Dzimauli, (2230 CD), 12 April 1980, *Van Wyk 4062* (PRU! 2 Sheets); ± 1 km from Dzamba on the way to Rambuda, (2230 CD), 04 December 1980, *Van Wyk 4085* (PRU! 3 Sheets); Tshirovho River, Mohovho-hovho Waterval, (2230 CD), 13 April 1980, *Van Wyk 4154* (PRU! 2 Sheets); Venda region, Tate Vondo, Mohovho-hovho waterfall, 2 December 1980, *Van Wyk 4275* (PRU!, 7 sheets); Thathe Vondo Forest Reserve, next to road between Wyllie's Poort and Thohoyandou immediately west of Thathe Vondo, elevation 985 m, (2230 CD), 23 March 1994, *Van Wyk BSA 1980* (PRU!); Sibasa District, Venda, at FM tower north of Thengwe, elevation 1015 m, 29 March 1994, *Van Wyk BSA 1994* (PRU!); Eastern Soutpansberg, east of Gundani village towards telecom. aerial, elevation 993 m, -22,64972222°S, -30.59944444°E, 07 September 2008, *Burrows 10604* (BNRH!); Eastern Soutpansberg, on road from Mufulwi to Tshixwadza, stream before (east of) Tshumulungwi, elevation 993 m, -22.70944444°S, 30.48138889°E, 07 September 2008, *Burrows 10610* (BNRH!); Eastern Soutpansberg, East of Masakadza, unpaved road along ridgetop of Gundani village, ca. 2 km West of cellphone tower, elevation 989 m, -22.64972222°S, 30.59944444°E, 26 September 2013, *Burrows et al. 13706* (BNRH, NU!); Eastern Soutpansberg, road from Mufulwi to Tshumilungwi, elevation 993 m, -22.7094444°S, 30.48138889°E, 26 September 2013, *Burrows et al., 13710* (NU!); Eastern Soutpansberg, Entabeni pine plantation (Komatiland), edge of pool below waterfall on dam wall formed by quartzitic rock outcrop, elevation 1021 m, -22.89527778°S, 30.37055556°E, 25 September 2013, *Burrows et al., 13712* (NU!); Eastern Soutpansberg, Mavhuwa to Tshixwadza road, elevation 1201 m, -22.75416667°S, 30.36166667°E, 28 November 2013, *Burrows & Burrows 13903* (BNRH!).

Distribution and habitat:— *Memecylon* sp. nov. 3 is known from 10 localities in the Soutpansberg, Limpopo province (Fig. 6.1.). The trees are found in streamside forests, in the vegetational mosaic described as "Soutpansberg Mountain Bushveld", and in "Northern Mistbelt Forest" (Rutherford et al., 2006) at elevations from 920 to 1300 m. The species is locally common only in some of the known locations, while in other localities it is quite rare (Stone, pers. obs.).

Phenology:—Flowering recorded in late September to early December; immature fruits in early September and early February to late June.

Conservation status:— *Memecylon* sp. nov. 3 is known from 10 localities with an extent of occurrence (EOO) of 850 km^2 and area of occupancy (AOO) of 36 km^2 and (assuming a 4 km^2 grid cell size). Most collections were made in tribal land (Gundani Village, Dzamba, Thengwe and Sibasa District), along roadsides and riverine forest, where the habitat is unprotected. The only protected location is the Komatiland site which is at the base of a waterfall in a commercial tree plantation is currently secure .The Entabeni State Forest probably also receives some degree of protection. Forests in Limpopo province are generally threatened by anthropogenic activities, as many people who live in rural areas surrounding forests continually utilize forest products e.g. wood harvesting for fuel, building materials, woodcarving, traditional medicines, and forests are cleared for agriculture (Hahn, 2004). Although these threats are not currently high, as human population pressure increases, so will the level of threat to the known populations. *Memecylon* sp. nov. 3 is thus provisionally assessed as "Vulnerable" [B1a,b(iii) + B2a,b(iii)] according to the IUCN Red List Categories and Criteria (IUCN, 2012).

Diagnostic features:—*Memecylon* sp. nov. 3 differs from *M. natalense* by its ovate leaf-blades (versus broadly elliptic ovate and elliptic leaf-blades) obtuse ± rounded base (versus cuneate base) cymes ca. 6–10 mm (versus cymes ca. 4–6 (–10) mm); acutely apiculate corolla in buds (versus rounded to subacute corolla in buds); peduncles 5–8 (–10) mm (versus peduncles 1–4 mm) (Table 6.1.**)**.

Buffelskloof Herbarium (BNRH)
Lydenburg, Mpumalanga, South Africa

MELASTOMATACEAE ***DT&H No.:*** 5788000
Memecylon soutpansbergensis R.D.Stone

Locality: 22°43'50" S, 30°27'10" E Alt: 1124m 2230CD
South Africa, Limpopo Province: Eastern Soutpansberg, c. 5 km E of Tshumulungwi on road to Mufulwi.

Notes:
Dense 2 m treelet growing amongst rocks in bush clump on quartzites.

Veg. Type: Soutpansberg Mountain Bushveld (SVcb 21)
Collector: Burrows, J.E., Burrows, S.M.
No.: 13905 28 November 2013
Det.: Burrows, J.E. 28 November 2013 BNRH0006473

Figure 6.7. *Memecylon* sp. nov. 3 (*Burrows & Burrows 13905*, BNRH). (BNRH photo)

6.3. Conservation assessments

According to the IUCN (International Union for Conservation of Nature and Natural Resources) threat categories, the Mozambican and South African *Memecylon* were provisionally assessed as: *Memecylon incisilobum* and *M. aenigmaticum* Critically Endangered (CR); *M. nubigenum, M. rovumense, M.* sp. nov. 1 and *M.* sp. nov. 3 Vulnerable (VU), while *M. natalense, M. bachmannii* and *M.* sp. nov. 2 are of "Least Concern".

The most critically endangered species are the local endemics (*M. incisilobum* and *M. aenigmaticum*), with very narrow distribution range and small population sizes. The South African *M.* sp. nov. 1 has a narrow distribution range and small population size, although provisionally assessed as Vulnerable for the time being. Species like *M. natalense* and *M. bachmannii* are not in urgent need of conservation measures. However, their differences between the EOO and AOO is largely due to the naturally fragmented distribution of forested habitats in eastern South Africa (Naicker et al., 2016), and some of their populations in these fragmented forests are threatened. Hence, it would be advantageous to prioritise conserving these threatened populations at local level rather than focusing on the species as a whole. *Memecylon* sp. nov. 3 has a smaller EOO and AOO with virtually none of the known locations receiving any formal protection, thus this taxon must be prioritized for conservation. Additionally, it is quite evident that although conserved areas represent an appropriate way to conserve natural resources, more often they fail to effectively conserve biodiversity (Pressey et al., 2003). There is now a concern that natural dynamics could be perturbed within formally conserved areas (Margules and Pressey, 2000).

Amongst the common threats (uncontrolled fires and alien invasive vegetation) to forests, habitat destruction caused by forest clearing for agriculture is a serious problem in most forests. The success of conservation efforts depends upon the recognition that poverty can be a significant constraint on conservation. Thus, conservationists must do a better job at addressing the interconnectivity of global biodiversity conservation priorities with human poverty issues (Fisher and Christopher, 2007). *Memecylon.* sp. nov. 3 is the most threatened of the South African species because of its lack of occurrences in formally protected areas which makes it especially vulnerable to threats caused by increasing human population pressures.

Table 6.1. Comparison of geographic distribution and morphology between *Memecylon natalense*, *M. bachmannii* and three other, putative species of *M.* section *Buxifolia* in South Africa.

	M. natalense	***M. bachmannii***	***M.* sp. nov. 1**	***M.* sp. nov. 2**	***M.* sp. nov. 3**
Distribution	KwaZulu-Natal, Eastern Cape, Mpumalanga and Limpopo provinces	KwaZulu-Natal, Eastern Cape	KwaZulu-Natal province	Eastern Cape province	Limpopo province
Habit	Small trees 2–4 m (rarely to 15 m)	Shrub or small tree 3–4.5 m	Tree 4–10 (–12) m	Shrub or small tree 2–4.5 m	Shrubs and small trees 2–3 (–5) m
Leaf-blades shape	Broadly elliptic ovate to elliptic	Broadly ovate and ± suborbicular	Elliptic to obovate	Broadly elliptic-ovate ± suborbicular	Ovate to broadly ovate
Leaf apex shape	Acutely acuminate	Abruptly acuminate	Broadly and obtusely acuminate	Acutely acuminate	Acutely acuminate
Leaf base shape	Cuneate	Rounded and ± shallowly cordate	Cuneate	Cuneate ± rounded	Obtuse or rounded
Petiole length	0.5–4 mm	0.5–1 mm	1.5–3 mm	1–3 mm	0.5–2 mm
Peduncle length	Peduncle not compressed 1–4 mm	Dorsoventrally compressed apex dilated, 0.5–2 mm	Peduncle not compressed (0.5–) 3–5 (–6.5) mm	Dorsoventrally compressed 0.5–2 mm	Peduncle not compressed 5–8 (–10) mm
Floral bracteoles	Rapidly deciduous	3 big pairs of opposite-decussate bracteoles, persistent and clasping base of the hypantho-calyx	Rapidly deciduous	3 small pairs of opposite-decussate bracteoles, persistent and clasping base of the hypantho-calyx	Rapidly deciduous
Hypantho-caylx shape	Obconic	Broadly cupuliform	Obconic to cupulo-patellate	Campanulate	Obconic
Hypantho-calyx margin	Entire	Entire	Sinuate-dentate	Entire	Entire

Hypantho-Calyx-lobes	Broadly rounded to triangular, green or suffused with dark purple	Broadly subtriangular	Broadly rounded	Broadly rounded to subtriangular	Broadly rounded to triangular
Corolla in bud shape	Rounded to subacute 3–4 mm	Rounded	Rounded-apiculate	Rounded-apiculate	Acutely apiculate
Petals shape	Broadly ovate to suborbicular	Broadly ovate to subrhomboid	broadly ovate to suborbicular	Broadly ovate to subrhomboid	Broadly ovate to suborbicular
Anther connectives colour	White	White	Yellow	Not seen	White
Fruit shape	Ellipsoid	Ovoid	Subglobose	Ovoid	Ellipsoid
Calycinal Crown lobes shape	Broadly subacute to spreading	Broadly rounded to subtriangular	Rounded and scarious	Broadly rounded to subtriangulular	Broadly subacute to spreading

6.4. Key to the species of *Memecylon* in South Africa

1. Bracteoles rapidly deciduous; fruits subglobose to ± ellipsoid………………..……2

- Bracteoles persistent; fruits ± ovoid……………………………………….……………4

2. Leaf apex broadly and obtusely acuminate; corolla acutely apiculate in bud; hypantho-calyx margin sinuate-dentate, scarious. Occurs at Kosi Bay Nature Reserve, northeastern KwaZulu-Natal, South Africa..***M.* sp. nov. 1**

- Leaf apex acutely acuminate; corolla in bud rounded to subacute; hypantho-calyx margin entire...…...……3

3. Leaf-blades broadly elliptic ovate to elliptic; base cuneate; cymes ca. 4–6 (–10) mm; peduncles 1–4 mm. Sporadically distributed in the Eastern Cape and KwaZulu-Natal (South Africa), with some outlying populations in Limpopo and Mpumalanga provinces (SA)………. ……………..…………………………………......***M. natalense***

- Leaf-blades suborbicular to broadly ovate, base obtuse or nearly rounded; cymes ca. 6–10 mm, peduncles 5–8 (–10) mm. Known only from Soutpansberg, Limpopo province, (South Africa)…………... ……………………..……***M.* sp. nov. 3**

4. Leaf-blades broadly rounded to ± suborbicular, (35–) 54–85 (–100) × (37–) 40–75 (–90) mm; obtuse ± shallowly cordate base 20–45 (–53) mm; lower pair of floral bracteoles (1–) 3 × 1–3 mm; middle pair of floral bracteoles 2–4 × 2 (–4) mm; upper pair of floral bracteoles 3–5 × 2.5 mm; fruit size 4–10 (–14) × 4–6 (–10) mm in diameter. Known from KwaZulu-Natal and Eastern Cape provinces (South Africa).........***M. bachmannii***

- Leaf-blades broadly elliptic-ovate to ± suborbicular, 35–45 (–55) × (25–) 30–35 (–40) mm; cuneate ± obtuse base 14–30 mm; lower pair of floral bracteoles (0.5–) 1 × 1.5 mm; middle pair of floral bracteoles 2 × 1.5 (–2) mm; upper pair of floral bracteoles 2 × 3 mm; fruit size 4–7 × 3–5 mm in diameter. Known only from Eastern Cape province (South Africa)……..……….……….…………………………………......***M.* sp. nov. 2**

CHAPTER 7: CONCLUSIONS

7.1. Taxonomy of the *Memecylon natalense* species complex in southern Africa

Recent molecular studies (Stone, 2014; Stone et al., 2017a) have revealed that *M. natalense* as previously circumscribed is not a monophyletic group and includes some geographically outlying populations warranting recognition as distinct evolutionary lineages. Prior to these studies, there had not been any in-depth research on *Memecylon* in southern Africa, and the previous works of Fernandes and Fernandes, (1972; 1978; 1980) are outdated. The present work has substantially advanced our knowledge of the evolutionary history, species boundaries and conservation status within the *Memecylon natalense* species complex in SA and Mozambique (Stone et al., 2017a). It has also improved our scientific knowledge for better-informed biodiversity assessments and strategies aimed at conservation of natural habitats where these species occur.

7.2. Future research

Some aspects of this study only used fruiting specimens, because not all the taxa had collections that were well represented by flowering material. Hence, additional field collections of *M. rovumense* and *M. aenigmaticum* flowering material would make it possible to carry out the phenetic and cladistic analyses on flowering specimens of all taxa.

As far as phylogenetics is concerned, it would be interesting to perform a molecular analysis of *M. natalense* from the Wolkberg Wilderness Area in Limpopo. Another interesting species to sample would also be *M. aenigmaticum*, which is closely related and morphologically similar to *M. rovumense* (a putative homoploid hybrid species between *M. fragran*s and *M. torrei*).

7.3. Conclusion

This study was set out to increase our knowledge of the genus *Memecylon* in southern Africa. The results indicate that indeed *Memecylon natalense* species-complex had cryptic species that were often confused as the South African *M. natalense*. Overall, seven new species have been described namely: *M. incisilobum*, *M. nubigenum*, *M. rovumense*, *M. aenigmaticum*, *M.* sp. nov. 1, *M.* sp. nov. 2 and *M.* sp. nov. 3. Molecular methods are good at detecting cryptic species but in many cases, this avenue of research fails to recover evolutionary history of recently and rapidly diverged species. The molecular studies published thus far have employed only a few DNA markers (nrDNA

ITS1, ITS2, 5’ETS). It would be advantageous to increase the number of markers or to use a newly developed genomic tools. This might be helpful in resolving the evolutionary history/relationships of this species complex and close relatives. Vegetative and fruit morphology have proven to be of great diagnostic value and useful in delimiting the members of the *M. natalense* species-complex based on the diagnostic species concept.

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Appendix A: List of specimens used in the phenetic analysis. Herbarium acronyms follow *Index* Herbariorum (http://sweetgum.nybg.org/ih/)

OTU	Collector and number	Herbarium
1. *M. aenigmaticum*	*Timberlake 5574*	**K**
2. *M.* sp. nov. 2	*Gordon-Gray 2005*	**NU**
3. *M.* sp. nov. 2	*Styles 4770*	**NU**
4. *M.* sp. nov. 2	*Styles 4771*	**NU**
5. *M.* sp. nov. 2	*Jenkins s.n.*	**PRE**
6. *M.* sp. nov. 2	*Stone et al. 2800*	**NU**
7. *M.* sp. nov. 2	*Stone et al. 2802*	**NU**
8. *M. bachmannii*	*Van Wyk & Matthews 7724*	**NH**
9. *M. bachmannii*	*Van Wyk 1579*	**PRU**
10. *M. bachmannii*	*Abbott 49*	**PRU**
11. *M. bachmannii*	*Cunningham 2495*	**NU**
12. *M. bachmannii*	*Stone & Potgieter 2689*	**NU**
13. *M. bachmannii*	*Cooper 290*	**NH**
14. *M. bachmannii*	*Stone et al. 2766*	**NU**
15. *M. bachmannii*	*Style 1573*	**NU**
16. *M. bachmannii*	*Style 4769*	**NU**
17. *M. bachmannii*	*Styles1579*	**PRU**

18. *M. bachmannii*	*Miller 5439*	**PRE**
19. *M. bachmannii*	*Nicolson 1462*	**PRE**
20. *M. bachmannii*	*Grieve 5*	**UDW**
21. *M. bachmannii*	*van Wyk BSA 2577*	**PRE**
22. *M. bachmannii*	*Strey 6502*	**NU**
23. *M. incisilobum*	*Matimele & Tokura 2208*	**BNRH; NU**
24. *M.* sp. nov. 1	*Stone et al. 2806*	**NU**
25. *M.* sp. nov. 1	*Stone et al. 2807*	**K**
26. *M. natalense*	*van Wyk 2627*	**K**
27. *M. natalense*	*Bayer 6827*	**PRE**
28. *M. natalense*	*Edwards 2488*	**PRE**
29. *M. natalense*	*Stone et al. 2771*	**NU**
30. *M. natalense*	*Styles 1584*	**NU**
31. *M. natalense*	*Moll 3313*	**PRE**
32. *M. natalense*	*Moll 5625*	**K**
33. *M. natalense*	*Stone et al. 2794*	**nu**
34. *M. natalense*	*Garland s.n.* (23 Nov 1969)	**NU**
35. *M. natalense*	*I. B. P. E. 786*	**PRE**
36. *M. natalense*	*Burrows 9466*	**BNRH**
37. *M. natalense*	*Ross 1890*	**PRE**

38. *M. natalense*	*Moll & Müller 5672*	**PRE**
39. *M. natalense*	*Ngwenya 2327*	**NH**
40. *M. natalense*	*Stone & S. Cassimje 2764*	**NU**
41. *M. natalense*	*Stone & Cassimjee 2765*	**NU**
42. *M. natalense*	*Stone et al. 2768*	**NU**
43. *M. natalense*	*Stone et al. 2690*	**NU**
44. *M. natalense*	*Stone et al. 2771*	**NU**
45. *M. natalense*	*Wells & Edwards 15*	**PRE**
46. *M. nubigenum*	*Muller 1474*	**K**
47. *M. nubigenum*	*Torre & Correia 15956*	**K**
48. *M. nubigenum*	*Blackmore et al. 1512*	**K**
49. *M. nubigenum*	*Chapman 8098*	**K**
50. *M. nubigenum*	*Chapman 9292*	**K**
51. *M. nubigenum*	*Nothale & Patel 717*	**K**
52. *M. rovumense*	*Clarke 56*	**K**
53. *M.* sp. nov. 3	*Van Wyk 3634*	**PRE**
54. *M.* sp. nov. 3	*Van Wyk 4085*	**PRU**
55. *M.* sp. nov. 3	*Van Wyk 4154*	**PRU**
56. *M.* sp. nov. 3	*Venter 11149*	**NU**
57. *M.* sp. nov. 3	*Hemm s.n.*	**K**

58. *M.* sp. nov. 3	*Burrows 10610*	**NU**
59. *M.* sp. nov. 3	*Van Wyk BSA 1980*	**PRU**
60. *M.* sp. nov. 3	*Van Wyk BSA 1994*	**PRU**
61. *M.* sp. nov. 3	*Van Wyk BSA 2019*	**PRU**

Appendix B: Character matrix used in the phenetic analysis. Character-states are represented by numbers in Table 3.1. OTU numbers represent specimens listed in Appendix A.

	Characters																			
OTUs	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
1	1	5	1	0	0	2	0	0	3	2	1	0	0	1	0	?	0	1	1	0
2	0	3	0	0	0	3	1	0	0	1	1	0	1	1	0	1	1	0	1	0
3	1	4	0	0	0	3	0	0	0	1	1	0	1	1	0	1	1	0	1	0
4	1	3	0	0	0	3	1	0	0	1	1	0	1	1	0	1	1	0	1	0
5	0	3	0	0	0	3	1	0	0	1	1	0	1	1	0	1	1	0	1	0
6	1	3	0	0	0	3	0	0	0	1	1	0	1	1	0	1	1	0	1	0
7	1	3	0	0	0	3	0	0	0	1	1	0	1	1	0	1	1	0	1	0
8	2	4	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0
9	2	4	0	0	2	0	0	1	0	1	1	0	1	1	0	1	1	0	1	0
10	0	4	0	0	2	0	0	0	0	1	1	0	1	1	0	1	1	0	1	0
11	2	6	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0
12	2	4	0	2	2	0	1	0	0	1	1	0	1	1	0	1	1	0	1	0
13	2	4	0	2	2	0	0	3	0	1	1	0	1	1	0	1	1	0	1	0
14	2	4	0	2	2	0	0	3	0	1	1	0	1	1	0	1	1	0	1	0
15	2	4	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0
16	2	4	0	0	2	0	0	0	0	1	1	0	1	1	0	1	1	0	1	0
17	2	4	0	2	2	0	1	0	0	1	1	0	1	1	0	1	1	0	1	0
18	2	4	0	0	2	0	1	2	0	1	1	0	1	1	0	1	1	0	1	0
19	2	4	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0
20	2	4	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0
21	2	6	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0
22	2	6	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0
23	1	1	0	2	1	1	2	2	0	1	1	2	1	0	1	1	1	0	1	1
24	0	1	0	0	1	1	1	0	0	1	1	2	1	1	1	1	0	0	1	0
25	0	1	0	0	1	1	1	0	0	1	1	2	1	1	1	1	0	0	1	0
26	2	3	0	0	0	3	0	0	0	1	1	0	1	1	1	0	0	0	1	0
27	0	3	0	0	0	3	1	0	0	1	1	0	1	1	1	0	0	0	1	0
28	2	3	0	0	0	3	1	0	2	1	1	1	1	1	0	0	0	0	1	0

29	2	3	0	0	0	3	1	0	2	1	1	0	1	1	0	0	0	0	1	0
30	2	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0
31	0	3	0	0	0	3	0	0	0	1	1	0	1	1	0	0	0	0	1	0
32	0	3	0	0	0	3	1	1	2	1	1	0	1	1	0	0	0	0	1	0
33	2	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0
34	2	3	0	0	0	3	0	0	0	1	1	0	1	1	0	0	0	0	1	0
35	1	3	0	0	0	3	1	0	2	1	1	0	1	1	0	0	0	0	1	0
36	0	3	0	0	0	3	0	1	0	1	1	0	1	1	0	0	0	0	1	0
37	1	3	0	0	0	3	1	0	0	1	1	0	1	1	0	0	0	0	1	0
38	0	3	0	0	0	3	1	0	0	1	1	0	1	1	0	0	0	0	1	0
39	1	3	0	0	0	3	1	1	0	1	1	1	1	1	0	0	0	0	1	0
40	2	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0
41	1	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0
42	2	3	0	0	0	3	0	0	2	1	1	0	1	1	0	0	0	0	1	0
43	0	3	0	0	0	3	1	1	2	1	1	0	1	1	0	0	0	0	1	0
44	2	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0
45	1	3	0	0	0	3	1	0	2	1	1	1	1	1	0	0	0	0	1	0
46	2	4	0	0	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0
47	0	4	0	1	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0
48	2	4	0	0	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0
49	0	4	0	1	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0
50	2	4	0	0	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0
51	2	4	0	0	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0
52	2	5	1	0	1	1	2	0	1	2	2	1	1	1	0	2	0	1	1	0
53	2	4	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0
54	1	4	0	0	0	3	0	0	2	1	1	1	1	1	0	0	0	0	1	0
55	2	4	0	0	0	3	1	0	2	1	1	1	1	1	0	0	0	0	1	0
56	1	4	0	0	0	3	0	0	0	1	1	1	1	1	0	0	0	0	1	0
57	1	4	0	0	0	3	0	0	2	1	1	1	1	1	0	0	0	0	1	0
58	1	4	0	0	0	3	0	0	2	1	1	1	1	1	0	0	0	0	1	0
59	2	4	0	0	0	3	1	0	2	1	1	1	1	1	0	0	0	0	1	0
60	0	4	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0
61	1	4	0	0	0	3	0	0	2	1	1	1	1	1	0	0	0	0	1	0

Appendix C: List of specimens used in the cladistic analysis. Herbarium acronyms follow Index Herbariorum (http://sweetgum.nybg.org/ih/).

OTUs	Collector and number	Accession
1. *M. aenigmaticum*	*Timberlake 5574*	**K**
2. *M.* sp. nov. 2	*Gordon-Gray 2005*	**NU**
3. *M.* sp. nov. 2	*Styles 4770*	**NU**
4. *M.* sp. nov. 2	*Styles 4771*	**NU**
5. *M.* sp. nov. 2	*Jenkins s.n.* (27 May 1970)	**PRE**
6. *M.* sp. nov. 2	*Stone et al. 2800*	**NU**
7. *M.* sp. nov. 2	*Stone et al. 2802*	**NU**
8. *M. bachmannii*	*Van Wyk & Matthews 7724*	**NH**
9. *M. bachmannii*	*Van Wyk 1579*	**PRU**
10. *M. bachmannii*	*Abbott 49*	**PRU**
11. *M. bachmannii*	*Cunningham 2495*	**NU**
12. *M. bachmannii*	*Stone & Potgieter 2689*	**NU**
13. *M. bachmannii*	*Cooper 290*	**NH**
14. *M. bachmannii*	*Stone et al. 2766*	**NU**
15. *M. bachmannii*	*Styles 1573*	**NU**
16. *M. bachmannii*	*Styles 4769*	**NU**

17. *M. bachmannii*	*Styles 1579*	**PRU**
18. *M. bachmannii*	*Miller 5439*	**PRE**
19. *M. bachmannii*	*Nicholson 1462*	**PRE**
20. *M. bachmannii*	*K. Grieve 5*	**UDW**
21. *M. bachmannii*	*P. van Wyk BSA 2577*	**PRE**
22. *M. bachmannii*	*Strey 6502*	**NU**
23. *M. incisilobum*	*Matimele & Tokura 2208*	**BNRH; NU**
24. *M.* sp. nov. 1	*Stone et al. 2806*	**NU**
25. *M.* sp. nov. 1	*Stone et al. 2807*	**K**
26. *M. natalense*	*Van Wyk 2627*	**K**
27. *M. natalense*	*Bayer 6827*	**PRE**
28. *M. natalense*	*Edwards 2488*	**PRE**
29. *M. natalense*	*Stone et al. 2771*	**NU**
30. *M. natalense*	*Styles 1584*	**NU**
31. *M. natalense*	*Moll 3313*	**PRE**
32. *M. natalense*	*Moll 5625*	**K**
33. *M. natalense*	*Stone et al. 2794*	**NU**
34. *M. natalense*	*Garland s.n.* (23 Nov 1969)	**NU**
35. *M. natalense*	*I. B. P. E. 786*	**K**
36. *M. natalense*	*Burrows 9466*	**BNRH**

37. *M. natalense*	*Ross 1890*	**PRE**
38. *M. natalense*	*Moll & Müller 5672*	**PRE**
39. *M. natalense*	*Ngwenya 2327*	**NH**
40. *M. natalense*	*Stone & Cassimjee 2764*	**NU**
41. *M. natalense*	*Stone & Cassimjee 2765*	**NU**
42. *M. natalense*	*Stone et al. 2768*	**NU**
43. *M. natalense*	*Stone et al. 2690*	**NU**
44. *M. natalense*	*Stone et al. 2771*	**NU**
45. *M. natalense*	*Wells & Edwards 15*	**PRE**
46. *M. nubigenum*	*Müller 1474*	**K**
47. *M. nubigenum*	*Torre & Correia 15956*	**K**
48. *M. nubigenum*	*Blackmore et al. 1512*	**K**
49. *M. nubigenum*	*Chapman 8098*	**K**
50. *M. nubigenum*	*Chapman 9292*	**K**
51. *M. nubigenum*	*Nothale & Patel 717*	**K**
52. *M. rovumense*	*Clarke 56*	**K**
53. *M.* sp. nov. 3	*Van Wyk 3634*	**PRE**
54. *M.* sp. nov. 3	*Van Wyk 4085*	**PRU**
55. *M.* sp. nov. 3	*Van Wyk 4154*	**PRU**
56. *M.* sp. nov. 3	*Venter 11149*	**NU**

57. *M.* sp. nov. 3	*Hemm s.n.* (30 June 1978)	**K**
58. *M.* sp. nov. 3	*Burrows 10610*	**NU**
59. *M.* sp. nov. 3	*Van Wyk BSA 1980*	**PRU**
60. *M.* sp. nov. 3	*Van Wyk BSA 1994*	**PRU**
61. *M.* sp. nov. 3	*Van wyk BSA 2019*	**PRU**
62. *M. cogniauxii*	*Hemp 5906*	**UBT**
63. *M. deminutum*	*Hemp 3075*	**UBT**

Appendix D: Character matrix used in the cladistic analysis. Characters and character states are represented by numbers in Table 4.1. OTUs numbers represents specimens used listed in Appendix C.

	Characters																					
OTUs	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
1	1	5	1	0	0	2	0	0	3	2	1	0	0	1	0	?	0	1	1	0	1	1
2	0	3	0	0	0	3	1	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
3	1	4	0	0	0	3	0	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
4	1	3	0	0	0	3	1	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
5	0	3	0	0	0	3	1	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
6	1	3	0	0	0	3	0	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
7	1	3	0	0	0	3	0	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
8	2	4	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	1	1
9	2	4	0	0	2	0	0	1	0	1	1	0	1	1	0	1	1	0	1	0	1	1
10	0	4	0	0	2	0	0	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
11	2	6	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	1	1
12	2	4	0	2	2	0	1	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
13	2	4	0	2	2	0	0	3	0	1	1	0	1	1	0	1	1	0	1	0	1	1
14	2	4	0	2	2	0	0	3	0	1	1	0	1	1	0	1	1	0	1	0	1	1
15	2	4	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	1	1
16	2	4	0	0	2	0	0	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
17	2	4	0	2	2	0	1	0	0	1	1	0	1	1	0	1	1	0	1	0	1	1
18	2	4	0	0	2	0	1	2	0	1	1	0	1	1	0	1	1	0	1	0	1	1
19	2	4	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	1	1

20	2	4	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	1	1
21	2	6	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	1	1
22	2	6	0	2	2	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	1	1
23	1	1	0	2	1	1	2	2	0	1	1	2	1	0	1	1	1	0	1	1	1	1
24	0	1	0	0	1	1	1	0	0	1	1	2	1	1	1	1	0	0	1	0	1	1
25	0	1	0	0	1	1	1	0	0	1	1	2	1	1	1	1	0	0	1	0	1	1
26	2	3	0	0	0	3	0	0	0	1	1	0	1	1	1	0	0	0	1	0	1	1
27	0	3	0	0	0	3	1	0	0	1	1	0	1	1	1	0	0	0	1	0	1	1
28	2	3	0	0	0	3	1	0	2	1	1	1	1	1	0	0	0	0	1	0	1	1
29	2	3	0	0	0	3	1	0	2	1	1	0	1	1	0	0	0	0	1	0	1	1
30	2	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
31	0	3	0	0	0	3	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1
32	0	3	0	0	0	3	1	1	2	1	1	0	1	1	0	0	0	0	1	0	1	1
33	2	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
34	2	3	0	0	0	3	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1
35	1	3	0	0	0	3	1	0	2	1	1	0	1	1	0	0	0	0	1	0	1	1
36	0	3	0	0	0	3	0	1	0	1	1	0	1	1	0	0	0	0	1	0	1	1
37	1	3	0	0	0	3	1	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1
38	0	3	0	0	0	3	1	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1
39	1	3	0	0	0	3	1	1	0	1	1	1	1	1	0	0	0	0	1	0	1	1
40	2	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
41	1	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
42	2	3	0	0	0	3	0	0	2	1	1	0	1	1	0	0	0	0	1	0	1	1
43	0	3	0	0	0	3	1	1	2	1	1	0	1	1	0	0	0	0	1	0	1	1
44	2	3	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
45	1	3	0	0	0	3	1	0	2	1	1	1	1	1	0	0	0	0	1	0	1	1
46	2	4	0	0	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0	1	1
47	0	4	0	1	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0	1	1
48	2	4	0	0	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0	1	1
49	0	4	0	1	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0	1	1
50	2	4	0	0	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0	1	1
51	2	4	0	0	0	3	1	0	0	1	1	1	1	0	0	3	0	0	0	0	1	1
52	2	5	1	0	1	1	2	0	1	2	2	1	1	1	0	2	0	1	1	0	1	1
53	2	4	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
54	1	4	0	0	0	3	0	0	2	1	1	1	1	1	0	0	0	0	1	0	1	1
55	2	4	0	0	0	3	1	0	2	1	1	1	1	1	0	0	0	0	1	0	1	1
56	1	4	0	0	0	3	0	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
57	1	4	0	0	0	3	0	0	2	1	1	1	1	1	0	0	0	0	1	0	1	1
58	1	4	0	0	0	3	0	0	2	1	1	1	1	1	0	0	0	0	1	0	1	1
59	2	4	0	0	0	3	1	0	2	1	1	1	1	1	0	0	0	0	1	0	1	1
60	0	4	0	0	0	3	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1
61	1	4	0	0	0	3	0	0	2	1	1	1	1	1	0	0	0	0	1	0	1	1
62	2	7	1	0	3	2	2	0	0	1	0	3	1	1	0	1	0	0	?	0	0	0
63	0	0	2	0	2	0	0	1	1	0	0	0	1	0	?	?	0	0	?	0	0	0

Appendix E

List of apomorphies in the cladistic analysis. CI = Consistency Index.

Branch	**Clade**	**Character**	**Steps**	**CI**	**Change in character-states**
node_84 --> node_83	*Memecylon* Sect. *Buxifolia* **‘A’**	2	1	0.600	0 ==> 3
		11	1	1.000	0 ==> 1
		21	1	1.000	0 ==> 1
		22	1	1.000	0 ==> 1
node_83 --> node_64	*M. rovumense*+*M. aenigmaticum* **‘B’**	2	1	0.600	3 ==> 5
		9	1	0.250	0 ==> 1
		10	1	1.000	1 ==> 2
		16	1	0.273	0 ==> 2
		18	1	1.000	0 ==> 1
node_70 --> node_69	*M. bachmannii* **‘C’**	4	1	0.500	0 ==> 2
		7	1	0.125	0 ==> 1
		8	1	0.333	1 ==> 2
node_82 --> node_73	*M. incisilobum*+ *M.* sp. nov. 1 **‘D’**	1	1	0.083	2 ==> 0
		2	1	0.600	3 ==> 1
		5	1	0.600	0 ==> 1
		6	1	0.600	3 ==> 1
		12	1	0.214	0 ==> 2
		15	1	0.333	0 ==> 1
		16	1	0.273	0 ==> 1
node_78 --> node_77	*M. nubigenum* **‘E’**	14	1	0.333	1 ==> 0
		16	1	0.273	0 ==> 3
		19	1	1.000	1 ==> 0