Warneckea parvifolia (Melastomataceae–Olisbeoideae), a new “sand-forest” endemic from northeastern KwaZulu-Natal (South Africa) and southernmost Mozambique, and a phylogenetic analysis of eastern and southern African representatives of W. section Warneckea

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ABSTRACT

Warneckea populations from “sand-forest” or “sand-thicket” habitats in Tembe Elephant Park, South Africa, and Licuati Forest Reserve in adjacent southern Mozambique were previously thought to be a small-leaved form of W. sousae, which typically includes larger-leaved plants ranging from central Mozambique northward to Tanzania. We examine this hypothesis using molecular and morphological evidence. Maximum-likelihood phylogenetic analysis of combined nDNA ETS and ITS sequence data failed to resolve W. sousae and the Maputaland populations as an exclusively monophyletic group. Instead, the Kenyan endemic W. mouririifolia was strongly supported as the sister species of W. sousae, and the Maputaland plants were resolved in a separate, strongly supported clade together with populations of an as-yet undetermined Warneckea species from northern Mozambique. A hypothesis of exclusive monophyly for the plants from Tembe and Licuati had moderate support in separate ETS and ITS1 analyses (bootstrap proportions of 88% and 81%, respectively). Statistically significant differences in leaf dimensions and internode length were found between the Maputaland plants and typical W. sousae. We conclude that the populations from Tembe and Licuati represent a distinct species, which we describe as W. parvifolia. The species differs from W. sousae in having shorter internodes (mostly 5–25 mm not 10–80 mm long), smaller leaves (mostly 14–32 × 8–19 mm not 40–76 × 22–52 mm), shorter pedicels (mostly 1–1.5 mm not 1.5–6 mm long), smaller flowers (hypanthium 1 × 1.5–1.75 mm not 1.5–2 × 2 mm; calyx lobes 0.5 mm not 0.75 mm long; staminal filaments 3–4 mm not 5 mm long; style 4–5 mm not 9 mm long), and globose fruit (not obovoid). An IUCN conservation status of Endangered (EN) B1a, b(ii, iii) is indicated for W. parvifolia, due to its limited distribution and projected declines in its habitat quality and area of occupancy.

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1. Introduction

Molecular phylogenetics holds much promise as a method for discovering previously undetected biodiversity at and near the species level (Baldwin, 2000). This is especially true when the phylogenetic approach is augmented with evidence from morphology and ecogeography. Lineages identified by molecular means are not necessarily morphologically cryptic: in some cases they may represent morphologically distinctive taxa that have been previously treated within more broadly circumscribed species. Integrated approaches to discovering fine-scale biodiversity should lead to a refined system of classification, and also to better-informed biodiversity assessments and strategies aimed at conservation of rare species.

Here we consider the circumscription of the taxon originally described as Memecylon sousae A. Fern. & R. Fern. and recently transferred to the genus Warneckea as W. sousae (A. Fern. & R. Fern.) A.E. van Wyk (Coates Palgrave, 2002). When first described, W. sousae was known from just four collections in Mozambique (Fernandes and Fernandes, 1972). The first report of this species from South Africa is that of Ross (1976), based on collections by Prof. Eugene Moll in “sand forest” 6–7 km west of Muzi in what is now the Tembe Elephant Park. The leaves of the collection Moll & Nel 5592 (K, MO, PRE) were described as up to 35 × 17 mm and “significantly smaller” than those of W. sousae, which had been described as having leaves 30–90 × 15–65 mm. Ross (1976) considered that the Tembe plants might represent an undescribed species if it could be shown that their leaves were consistently smaller than those of typical W. sousae, but the leaves in Moll & Müller 5690 (K, NH, NU) were more variable in size, ranging up to 56 × 38 mm, thus matching those of typical W. sousae. On the basis of these observations, Ross (1976) concluded that the Tembe plants fall within the range of variation of W. sousae.

Stone and Andreasen (2010) published a molecular phylogeny of the Afro-Madagascan genus Warneckea. Among the DNA sequences included in that study were those obtained from a collection of typical...
W. sousae from northern Mozambique (Luke 10168, CAS, EA, K). These results showed that W. sousae belongs in W. section Warneckea (a group that includes other Warneckea species from East Africa, Madagascar, and Mauritius), but no populations from South Africa or extreme southern Mozambique were included in the study.

We analyse new molecular and morphological evidence to assess whether the small-leaved populations from South Africa and extreme southern Mozambique are appropriately treated as conspecific with Warneckea sousae. The molecular data comprise sequences from the rDNA ETS and ITS regions, which have proven to be informative about species-level relationships in other angiosperm groups (Baldwin et al., 1995; Baldwin and Markos, 1998). At the morphological level, we have made comparative measurements of leaf dimensions, internode length, and floral and fruit dimensions based on herbarium material. We conclude that the Warneckea plants from “sand-forest” and “sand-thicket” in South Africa and extreme southern Mozambique are a distinct species, which we describe here as W. parvifolia.

2. Materials and methods

2.1. Plant material and taxonomic sampling

Four Warneckea samples were collected in Tembe Elephant Park, South Africa and one sample from Licuati Forest Reserve in southern Mozambique (Table 1). Leaf samples for DNA analysis were initially dried in silica-gel (Chase and Hills, 1991), and the corresponding voucher information is provided in Table 1.
herbarium voucher was deposited in the Bevis Herbarium (NU). New rDNA sequences were also obtained from samples of *W.* fascicularis (*Van der Burgt* 1120, K), typical *W.* sousae (*Luke* 13796, EA), and an undetermined *Warneckea* species from Cabo Delgado Province in northern Mozambique (*Luke* 13735, EA). GenBank accession numbers for newly reported sequences are in the range of KC897074 to KC897087.

In addition to the ETS and ITS sequences newly obtained for the current study, the phylogenetic analysis included previously published sequences (Stone and Andreasen, 2010) from *Warneckea* subgenus *Carinosae* (2 samples), *W.* section *Strychnoides* (2 samples), *W.* section *Guineenesis* (1 sample), and *W.* section *Warneckea* (14 samples). The sequences from *W.* subgenus *Carinosae* were selected as the outgroup, since this subgenus is the hypothesised sister-group of *W.* subgenus *Warneckea* (Stone, 2006; Stone and Andreasen, 2010).

2.2. DNA isolation, amplification, and sequencing

Total genomic DNAs were isolated and the rDNA ETS and ITS regions were amplified and sequenced as previously described by Stone and Andreasen (2010). Genomic DNAs were generally diluted at 1:10 or 1:50 in ultrapure water for use in polymerase chain reaction (PCR) experiments. The pool of amplicons from the initial PCR was directly sequenced with good results.

2.3. DNA sequence alignment

Forward and reverse sequences were assembled into contigs using the computer program ChromasPro, version 1.5 (Technelysium Pty. Ltd., Australia). In some cases the direct sequences exhibited site-specific polymorphisms. These were not common and were simply coded as polymorphic during contig assembly. Sequence alignment was generally unambiguous and was completed manually under a general criterion of maximising similarity (Simmons, 2004) while further aiming to treat indels as unique events (Morrison, 2006). ETS sequences were verified by a 40-nucleotide motif at the 3′ end, corresponding to the highly conserved 5′ end of the 18S rRNA gene (cf. Baldwin and Markos, 1998). After alignment of the ITS region, the middle part (i.e., the highly conserved 5.8S rRNA gene) was excised, leaving separate ITS1 and ITS2 data sets for further analysis. Previous authors have noted the presence of potentially informative length mutations (indels) in rDNA transcribed spacer sequences (e.g., Baldwin et al., 1995; Baldwin and Markos, 1998; Hershkovitz et al., 1999). In this study, gaps were treated as missing data and each unique indel was recoded as a binary character using the “simple indel coding method” of Simmons and Ochoterena (2000).

2.4. Phylogenetic analyses

Maximum-likelihood (ML) tree searches were implemented in the Windows version of the program GARLI 2.0 (Zwickl, 2006), with 100 rounds of topology, branch-length, and model-parameter optimisation from a random starting tree. The ETS, ITS1 and ITS2 input files each consisted of two partitions, the first partition containing the sequence alignment and the second the corresponding recoded indels to which a simple binary (restriction-site) model was applied. Selection of DNA substitution models was guided by non-nested comparisons using the Akaike information criterion (AIC) and Bayesian information criterion (BIC), both methods implemented in the program jModeltest 0.1.1 (Posada, 2008). Based on these results, an HKY+G substitution model was selected for the ETS and ITS1 regions (accounting for unequal base frequencies and bias in substitution rates favouring transitions over transversions, as well as among-site rate inconstancy following a gamma distribution with 4 discrete rate categories). For the ITS2 region, a GTR+G substitution model was selected (assuming different probabilities of change for each of six substitution types and gamma-distributed rate variation among sites). Internal clade support was assessed by non-parametric bootstrapping (Felsenstein, 1985), with ML analysis of 100 pseudoreplicates and 10 rounds of optimisation from a random starting-tree per pseudoreplicate.

Arguments for and against combining data have been well reviewed (de Queiroz et al., 1995). According to the philosophy of “conditional combination,” data from different partitions must first survive a test of heterogeneity (Bull et al., 1993; Huelsenbeck et al., 1996). One such test is to examine whether high bootstrap support for conflicting clades in phylogenetic trees is inferred by the separate data sets (de Queiroz, 1993). In the current study, separate ML analyses of ETS, ITS1, and ITS2 yielded tree topologies that are not significantly incongruent (results not shown). The separate data sets were thus combined in a single ETS + ITS1 + ITS2 analysis. For two samples (*Luke* 13735 and Netteh 4) the ITS1 and ITS2 sequences and gap characters were coded as missing data in the combined analysis (because no ITS sequences were obtained).

2.5. Morphological analyses

Morphological data were gathered from herbarium material kept at NU or obtained on loan from other institutions (see Acknowledgements). The morphological study was limited to comparisons between *Warneckea* collections from South Africa and southernmost Mozambique on the one hand (see Sections 5.1 and 5.6 for a list of specimens examined), and those of *W.* sousae from central to northern Mozambique on the other. The following specimens of *W.* sousae were examined for the morphological study:

Mozambique. CABO DELGADO: Quiterajo, SE edge of Guibouttia (Banana) forest, 24 Nov 2008, J.E. Burrows & S.M. Burrows 10703 (BNRH); Namacuhi (Banana) Forest, west of Quiterajo, 25 Nov 2008, J.E. Burrows & S.M. Burrows 10771 & 10772 (BNRH); 10 km NW of Palmia, Miculumo area, 8 Dec 2008, Timberlake et al. 5632 (BNRH).

NAMPULIA: Reserva da Cruse, between Matibane and Nacala, 19 Mar 2009, J.E. Burrows & S.M. Burrows 11240 (BNRH). SOFALA: Beira region, Chinzina, at the side way to the river Macalaau, 5 May 1957, Gomes e Sousa 4380 (isotypes K, PRE); Beira district, Cheringoma section, riverine forest, 15 July 1972, C.J. Ward 7970 (NU, UDW); ca. 25 km from Chinzina River crossing eastwards towards the sea, 8 Oct 2007, J.E. Burrows & S.M. Burrows 10162 (BNRH).

For each specimen, leaf length and width were measured for all leaves except those that were very young (hence not fully developed) or obviously deformed. Also measured was the length of all internodes except those of the current year’s growth. For each parameter the mean value was calculated for each specimen in order to avoid pseudoreplication. An independent-samples *t*-test was implemented using the computer program SPSS version 15 to test for significant differences in mean leaf dimensions and internode length between typical specimens of *W.* sousae and those collections from South Africa and southernmost Mozambique (*W.* parvifolia). Prior to this test, the assumption of normality was also tested for each group using the one-sample Kolmogorov–Smirnov test, and the assumption of equality of variances was tested using Levene’s test. Results suggested that the values of all three parameters were normally distributed. Equality of variances was met for leaf width but not for leaf length or internode length, so the values of these two parameters were log transformed. After log transformation the assumption of equality of variances was met.

3. Results

3.1. DNA sequence alignment

The ETS alignment had more than twice the number of parsimony-informative nucleotide sites as the ITS1 or ITS2 alignments (Table 2). This is understandable because the part of the ETS that was sequenced is more than twice as long as the other two spacer regions. The proportion of parsimony-informative nucleotide sites was approximately equal for ETS and ITS1, with a lower proportion seen in ITS2. The ETS
**3.2. Phylogenetic analyses**

Outgroup-rooted ML analysis of the combined sequence data plus binary-recoded gaps produced a single tree (Fig. 1) which is similar to the separate ETS, ITS1, and ITS2 trees (not shown) but is generally better resolved with increased internal support. Monophyly of Warneckea section Warneckea is strongly supported (bootstrap proportion of 100%), as is a subclade comprising the eastern and southern African species of section Warneckea, including *W. sousae* and the populations from South Africa and extreme southern Mozambique (bootstrap 97%).

The analysis strongly suggests (bootstrap 99%) that *W. mouririifolia* (a Kenyan endemic) is the sister species of *W. sousae* (northern Mozambique). These two taxa are in turn sister (bootstrap 87%) to a strongly supported clade (bootstrap 100%) comprising the populations from Tembe Elephant Park (South Africa) and Licuati Forest Reserve (Mozambique), hereafter referred to as *W. parvifolia* sp. nov., plus two populations of an undetermined Warneckea species from northern Mozambique (represented by *Luke 10155*, CAS, EA and *Luke 134735*, EA).

Although support for the monophyly of *W. parvifolia* is relatively weak (bootstrap 65%) in the combined analysis (Fig. 1), stronger support for this hypothesis is provided in the separate ETS and ITS1 analyses (bootstrap 88% and 81%, respectively; results not shown). Only in the separate ITS2 analysis was *W. parvifolia* not exclusively monophyletic, but this was weakly supported (53% bootstrap for a grouping of *Ntetha* 3 from Tembe and *Luke 10155* from northern Mozambique; results not shown).

**3.3. Morphological analyses**

Between *W. sousae* and *W. parvifolia* the mean leaf width and log-transformed leaf length and internode length were significantly different (Table 3). However, considerable overlap in leaf dimensions and internode length was also observed (Figs. 2 and 3). Of 82 leaves measured in *W. sousae*, 71% had dimensions in the range of 40–76 mm long × 22–61 mm wide, while in *W. parvifolia* there were 281 leaves measured with 81% ranging from 14–32 mm long × 5–22 mm wide. In two samples of *W. sousae* (*Ward 7970*, NU; *Tinberlake et al. 5632*, BNHR), a few smaller leaves 21–30 mm long × 16–18 mm wide were found. In *W. parvifolia*, only plants with small leaves 10–26 mm long × 5–17 mm wide were seen in the region also had the highest number of recoded gap characters and parsimony-informative gap characters.

**Table 2**

Summary of nrDNA ETS, ITS1 and ITS2 sequence variation among the samples of *Warneckea* included in this study.

|          | ETS | ITS1 | ITS2 |
|----------|-----|------|------|
| Number of sequences | 27  | 25   | 25   |
| Raw sequence length (nt) | 602–617 | 257–265 | 243–255 |
| Aligned sequence length (nt) | 635 | 274 | 263 |
| G–C content | 43–46% | 46–49% | 52–60% |

Pairwise sequence divergence (corrected)

|          | Sect. Warneckea | All sequences | Variable sites | Sect. Warneckea | All sequences | Informative sites | Sect. Warneckea | All sequences |
|----------|-----------------|---------------|----------------|-----------------|---------------|------------------|-----------------|---------------|
| 0–0.07    | 0–0.09          | 0–0.18        | 92 (14%)       | 35 (13%)       | 35 (13%)     | 174 (27%)        | 60 (9.4%)      | 28 (10%)      |
| 0–0.22    | 0–0.28          | 63 (23%)      | 63 (23%)       | 70 (27%)       |              |                  | 132 (21%)      | 54 (20%)      |
| 0–0.28    | 0–0.18          |              | 63 (23%)       | 70 (27%)       |              |                  | 132 (21%)      | 54 (20%)      |
| 0–0.25    | 0–0.18          |              | 63 (23%)       | 70 (27%)       |              |                  | 132 (21%)      | 54 (20%)      |
| 0–0.35    | 0–0.20          |              | 63 (23%)       | 70 (27%)       |              |                  | 132 (21%)      | 54 (20%)      |

Recoded gap characters 27 12 15

Informative gap characters 13 6 6

**Raw sequence length (nt)** 602

**G content** 43–46%, 46–49%, 52–60%

**Region also had the highest number of recoded gap characters and parsimony-informative gap characters.**

**4. Discussion**

Our null hypothesis was that the *Warneckea* populations in Tembe Elephant Park and Licuati Forest Reserve represent a small-leaved form of *W. sousae*, as treated by previous authors (Ross, 1976; A.E. van Wyk in Coates Palgrave, 2002). If this were true, then the smaller-leaved plants should share a recent common ancestor with *W. sousae*, to the exclusion of other species. Our phylogenetic analysis of combined ETS, ITS1 and ITS2 sequence data (Fig. 1) is not consistent with this scenario: although both groups of populations are placed within the same clade, *W. sousae* is well supported as sister to *W. mouririifolia*, with these two taxa in turn sister to a well-supported clade comprising the Tembe and Licuati plants plus two as-yet undetermined populations from northern Mozambique. At the morphological level, we have found statistically significant differences in leaf dimensions and internode length between typical *W. sousae* and the plants from Tembe and Licuati (*Table 3*), although substantial overlap is seen in the ranges of these characteristics.

From the molecular and morphological evidence presented thus far, one possible taxonomic conclusion is that *W. sousae* has been incorrectly treated as distinct from *W. mouririifolia*, and that all of the populations previously referred to *W. sousae* (including the plants from Tembe and Licuati) should be included within an expanded circumscription of *W. mouririifolia*. However, *W. mouririifolia* clearly differs from *W. sousae* in having leaf apices gradually and obtusely subacuminate or angustate (not rounded or shortly acuminate, the acumen broad and obtuse), inflorescences axillary and 3–5–flowered (vs flowers in dense glomerules at the defoliated nodes of the older branchlets), peduncles 1–6 mm long (vs inflorescences sessile), and flowers sessile (vs flowers on pedicels 1–4 mm long). Furthermore, our molecular analysis (Fig. 1) strongly suggests that *W. mouririifolia*, *W. Sousae*, and the populations from Tembe and Licuati represent distinct evolutionary lineages and should not be construed as interpopulational variation within a single species. We thus conclude that the *Warneckea* populations from Tembe and Licuati are a distinct species which needs to be formally described and named. This new taxon is morphologically similar to *W. sousae* but is diagnosably different (see *Section 5.3*).

**5. Species description**

**5.1. Warneckea parvifolia R.D. Stone & Ntetha, sp. nov.**

Type: South Africa. KwaZulu-Natal, 2732 (Ubombo); Tembe Elephant Park, (–AB), 3 Sep 1987, M.C. Ward 2681 (PRU, holo.; NH, iso.).

Evergreen shrub or small tree, 2.5–6 m tall; bark of trunk and older branches greyish white, finely longitudinally fissured; young branchlets quadrangular to narrowly quadrangular-alate or bisulate in section, pale reddish brown, with age becoming greyish white and terete; internodes mostly 5–25 mm long. Leaves (sub)coriaceous; petioles (0.5–) 1–1.5 (–2) mm long; blades elliptic to ovate, (10–)14–32 (–53) × (5–)8–19 (–36) mm, base cuneate to rounded or narrowly subcordate, apex rounded to shortly and obtusely...
acuminate, dark green above, paler beneath, longitudinally 3-nerved from base (or the larger leaves with an additional pair of weak, submarginal nerves), with 6–13 pairs of transverse veins, midnerve and lateral nerves impressed on upper surface, prominent on lower surface. Flowers in dense glomerules at defoliated nodes of older branchlets (rarely in leaf-axils), white, subsessile; pedicels concealed by bracts in bud, 0.5–1 mm long at anthesis and 1–2.2 (−3) mm long after anthesis; bracts imbricate-decussate, depressed-ovate to rhombiform, scarious, 0.5–0.75 mm long, narrowed at base, keeled on abaxial surface and cucullate-apiculate. Hypanthium campanulate to cupulapatellate, ±1 mm long and 1.5–1.75 mm diam., calyx lobes broadly ovate to transversally elliptic or rhombic, 0.5 × 1 mm, cucullate-apiculate and abaxially keeled, concealing corolla in bud. Petals spatulate-ovovate, 2 × 1–1.3 mm, narrowly cuneate at base. Stamens filaments 3–4 mm long; anthers ±0.8 mm long, thecae frontally positioned, lacking dorsal connective-gland. Style filiform, 4–5 mm long. Flowering time September to October. Fruits globose, ±8 mm diam., turning whitish but finally dark purple or almost black at maturity, crowned by persistent calyx lobes. Fruiting time November to December. Fig. 4.

Table 3

|                  | W. sousae (n = 10) | W. parvifolia (n = 19) | Value of test statistic (t) | p-value (2-tailed) |
|------------------|--------------------|------------------------|-----------------------------|-------------------|
| Leaf length (cm) | 5.5 ± 1.5          | 2.4 ± 0.8              | 6.9                         | p < 0.0001        |
| Leaf width (cm)  | 3.5 ± 0.6          | 1.4 ± 0.6              | 6.8                         | p < 0.0001        |
| Internode length (cm) | 2.3 ± 0.8 | 1.4 ± 0.4              | 4.3                         | p < 0.0001        |

Fig. 1. Outgroup-rooted maximum-likelihood tree from combined, mixed-model analysis of ETS, ITS1, and ITS2 sequences plus binary-recoded gaps. Numbers above branches indicate maximum-likelihood bootstrap proportions (values < 50% not shown). The scale bar represents the average number of nucleotide substitutions per site.
5.2. Distribution and habitat

*Warneckea parvifolia* is currently known from two populations, one in the 300-km² Tembe Elephant Park in extreme northeastern KwaZulu-Natal, South Africa, and the second in the 33-km² Licuati Forest Reserve in southernmost Mozambique (Fig. 5). At Tembe, it occupies the understorey of what has been called “short Sand Forest” (Matthews et al., 2001) but is conspicuously absent from areas of “tall Sand Forest.” It is locally common in the southwestern part of the park near Sihangwane, but elsewhere its occurrence is sporadic, with some sites of seemingly suitable habitat remaining unoccupied. The species was evidently not sampled in the phytosociological study of Gaugris (2008), which used small plots making it possible to overlook rare species. At Licuati, the species is frequently encountered within an extensive area of “sand-thicke” vegetation which rarely exceeds 5 m in height (Izidine et al., 2003). Satellite imagery of the coastal plain south of Delagoa Bay suggests there are additional, as-yet unsurveyed areas of sand-forest habitat existing outside of these formally protected areas (Google Earth, 2013). As a result, the overall extent and abundance of *W. parvifolia* remains unknown, although its status as a regionally endemic species is not in question.

Within the Maputaland centre of floristic endemism (Van Wyk, 1996; Matthews et al., 2001; Van Wyk and Smith, 2001), sand-forest has been characterised as a unique vegetation type occurring on ancient north–south trending sand dunes occupying the interior of the Mozambican coastal plain south of Delagoa Bay, at altitudes ranging from 50 to 120 m above sea level. At least 230 species and infraspecific taxa of plants have been documented as being endemic or near endemic to the Maputaland centre (Van Wyk, 1996). Of these Maputaland endemics, at least 27 taxa are restricted to sand-forest, including *W. parvifolia* (Matthews et al., 2001, as Memecylon sousae).

5.3. Similar species and diagnostic characters

*Warneckea parvifolia* is placed in *W.* section *Warnecka* (sensu Stone and Andreassen, 2010) by its combination of bark finely longitudinally fissured, inflorescences with persistent, imbricate-decussate bracts, flowers with well-developed calyx lobes concealing the corolla in bud, anther connective-gland absent, and embryo with just one fleshy cotyledon, the second obsolete.

*Warneckea parvifolia* was previously included in *W.* sousae but is distinguished by its relatively short internodes mostly 5–25 mm long, smaller leaves mostly 14–32 × 8–19 mm on short petioles mostly 1–1.5 mm long, smaller flowers (hypanthium 1 mm long × 1.5–1.75 mm diam., calyx lobes 0.5 mm long, staminal filaments 3–4 mm long, style 4–5 mm long), and globose fruit. In contrast, *W.* sousae has internodes mostly 10–45 (–60) mm long, leaf-blades mostly 40–76 × 22–52 mm, larger flowers (hypanthium 1.5–2 mm long × 2 mm diam., calyx lobes ± 0.75 mm long, staminal filaments 5 mm long, style 9 mm long), and mature fruit obovoid 9 × 7 mm. Petioles 2–6 mm long are seen in several collections of *W.* sousae, including the type, but in other material (Burrows 10772 & 11240, BNHR; Ward 7970, NU, UD) the petioles are consistently shorter, 1.5–2.5 mm, thus approaching those of *W.* parvifolia.

*Warneckea parvifolia* occurs well south of *W.* sousae sensu stricto, which ranges from Sofala Province in central Mozambique northward to the Pwani Region and Mafia Island in Tanzania (Fig. 5). The known populations of these species are separated from each other by a distance of at least 750 km. *Warneckea sousae* has been reported to occur on Inhaca Island near Maputo in southern Mozambique (Fernandes and Fernandes, 1972), based on Davidson 156 (SRGH), but we consider this report to be tentative since we have not seen the specimen.

Among other members of *W.* section *Warnecka*, *W.* parvifolia is most similar to *W.* sessilicarpa (A. Fern. & R. Fern.) Jacq.-Fél., known from two coastal sites in northern Mozambique (Fig. 5). Both species have relatively short internodes and small, short-petioled leaves, and dense, few- to many-flowered fascicles at the thickened nodes of the upper branchlets. *Warneckea sessilicarpa* differs in having flowers and fruits sessile (vs. pedicels 1–3 mm long in *W.* parvifolia). *Warneckea sessilicarpa* has also been reported from Madagascar (Jacques-Félix, 1985a,b), but further analysis has shown that the resemblance of these populations to the Mozambican species is only superficial, and the Madagascan plants will be described as a distinct species (R.D. Stone, unpublished results).

Our molecular phylogenetic analysis (Fig. 1) allies *W.* parvifolia with two populations of an as-yet undetermined *Warnecka* species from Cabo Delgado Province in northern Mozambique (represented by Luke 10155, CAS, EA; Luke 134735, EA). These populations have larger leaves resembling those of *W.* sousae and appear to represent a new species, but additional collections of fertile material are needed before it can be fully described.

5.4. Etymology

The species name *parvifolia* means “with small leaves.” In the revised edition of *Trees of Southern Africa*, the vernacular name is given as “Tonga false rose-apple” (Van Wyk in Coates Palgrave, 2002), in reference to the
Thonga people who historically inhabited the coastal plain south of Delagoa Bay. However, this name is no longer favoured by the local inhabitants, and has been abandoned in favour of Maputaland (Van Wyk, 1996; Van Wyk and Smith, 2001; Gaugris, 2008). We suggest the alternative vernacular name “Maputaland false rose-apple.”

5.5. Conservation status

During our field work at Tembe in June 2012, every Warneckea plant we observed showed signs of resprouting or coppicing after being utilised by elephants. The park boundaries have been fenced since 1989, limiting the movement of elephants and increasing their utilisation of sand-forest habitats with which they previously had no close association (Matthews et al., 2001; Gaugris, 2008). The utilisation of seedlings and saplings by smaller browsing animals might also limit future recruitment of woody plants at Tembe (Gaugris, 2008). However, without long-term monitoring there is really no evidence that elephants or other herbivores are responsible for the currently rather spotty distribution of W. parvifolia at Tembe.

Warneckea parvifolia is more abundant at Licuati where no elephant utilisation was observed, but this forest reserve is not very well protected against anthropogenic threats (Izidine et al., 2003). Warneckea parvifolia is known to exist at fewer than five locations with an extent of occurrence estimated to be greater than 100 km² but much less than 5000 km². In addition, future declines in its area of occupancy and degradation of its sand-forest habitat are projected in Tembe Elephant Park as a result of utilisation by elephants. A conservation status of Endangered (EN) B1a, b(ii, iii) is therefore recommended for W. parvifolia according to IUCN (2001) criteria.

5.6. Additional specimens examined

South Africa. KWAZULU-NATAL: 2632 (Bela Vista): 7 km west of Muzi (−DC), 24 Oct 1971, Moll & Nel 5592 (K, MO, PRE); 6 km W of Muzi (−CD), 7 Jun 1972, Moll & Müller 5690 (K, NH [3 sheets], NU, herb. Umtamvuna); Tembe Elephant Park (−CD), 25 Oct 1988, M.C. Ward 2406 (NH); Tembe Elephant Park (−DC), 7 Jun 1995, P. van Wyk BSA_2986 (PRU); Tembe Elephant Park, north-east quadrant

![Figure 4. Warneckea parvifolia. (A) Flowering branch; (B–C) leaves; (D) detail of lower leaf surface; (E) flower; (F) fruiting branch; (G) fruit, longitudinal section; (H) seed. Voucher specimens: (A–B, D–E) M.C. Ward 2091, NH; (C) Moll & Nel 5592, K; (F–H) Burrows et al. 11517, BNRH. Scale: (A–C, F) 10 mm; (D, G–H) 4 mm; (E) 1 mm.](image-url)
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