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Article in *Systematic Botany* · March 2017

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The Namib-Thar Desert Disjunction in *Dactyliandra* (Cucurbitaceae) is the Result of a Recent Introduction to India

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Communicating Editor: Chrissen E. C. Gemmill

Abstract—Depending on taxonomic concept, the genus *Dactyliandra* (Cucurbitaceae) comprises up to four species: two from Southwest Africa, *D. luederitziana* (Namibia) and *D. welwitschii* (Angola), and two very locally distributed and poorly known taxa from Northeast Africa, *D. nigrescens* and *D. stefanii*. In addition to these African populations, *D. welwitschii* was also reported as a possibly native species from the Thar desert of Northwestern India and Pakistan ca. 8,000 km away from the Namib range. A phylogenetic analysis of plastid and nuclear ribosomal ITS DNA sequences including all *Dactyliandra* species and *D. welwitschii* from the Thar desert revealed that this striking disjunction is of very recent origin. *Dactyliandra* is monophyletic only after exclusion of the East African taxa, which are best placed in *Trochomeria*. The species *Dactyliandra welwitschii* is monophyletic and includes the Indian plants, which group with a sample from an Angolan population. We hypothesize that this unexpected connection is a result of man-mediated introduction to India from Africa perhaps in the times of the slave trade. The new combinations *Blastania lucorum* and *Trochomeria nigrescens* are published here.

Keywords—*Blastania*, continental tracks, molecular clock, Saharo-Sindian desert belt, Siddi, *Trochomeria*.

The genus *Dactyliandra* Hook.f. was originally described by the British botanist Joseph D. Hooker in 1871 from material collected in Angola, southwestern Africa (Hooker 1871). The species was described as *D. welwitschii* Hook.f. to honor the Austrian explorer and botanist Friedrich Welwitsch (1806–1872) who had collected the type material. Further fieldwork revealed that its distribution is restricted to the Namib region of Angola and adjacent Namibia. The Namibian plants (Fig. 1) seemed to be morphologically slightly different (3-lobed leaves instead of 5- to 7-lobed leaves) when Cogniaux studied the very limited number of herbarium collections available to him and therefore described them as a second species, *D. luederitziana* Cogn. (Cogniaux 1916). This concept, however, was not accepted and the following authors treated all Southwest African plants as one single species *D. welwitschii* (e.g. Meeuse 1962, Gibbs Russell et al. 1987).

It was a big surprise when almost a century after Welwitsch's discovery, the Indian botanist M. Bhandari found *Dactyliandra* plants morphologically matching *D. welwitschii* in Rajasthan about 8,000 km away from the species's previously known distribution range (Bhandari and Singh 1964; Fig. 2). In Rajasthan, the species was reported to be locally common as a climber over *Capparis* L. bushes and in hedges but Bhandari & Singh (1964) also suggested that it might have been overlooked or confused with the similar looking *Blastania garcini* (L.) Cogn. (syn. *Ctenolepis garcini* (L.) C. B. Clarke) and might be more widespread. Later, the species was indeed also found in the Kirthar Range on the Pakistani side of the border (Khatoun 2006). This suggested that the total Thar region population might be bigger and cover a relatively large range, which could indicate an indigenous status. The case was widely cited as an example of an extreme disjunction and even used by panbiogeographers as evidence for “tracks” between continents (Craw et al. 1999). However, doubts about its native status remained and a human-mediated introduction to the Thar region could not be excluded.

Less attention was given to an additional species of *Dactyliandra*, *D. nigrescens* C. Jeffrey (Jeffrey 1965), which was described at the same time from Eastern Africa, roughly in the middle of the route from Northern India to Southwestern

Africa. A further East African species, *D. stefanii* (Chiov.) C. Jeffrey, also remained more or less unnoticed. *Dactyliandra stefanii* had been described by Chiovenda as a species of *Coccinia* Wight & Arn. (Chiovenda 1917), it was later transferred to *Trochomeria* Hook.f. by Jeffrey in 1962 and finally moved to *Dactyliandra* in 1985 (Jeffrey 1962, 1985). These East African plants reduced the extreme disjunction in the genus but at the same time called into question the species circumscriptions in *Dactyliandra*, with the populations of the two extreme ends of the range being attributed to the same species and two different species living more or less in sympatry in between (Fig. 2).

Family-wide phylogenetic analyses placed *D. welwitschii* in the tribe Benincaseae in a well-supported clade together with representatives of the genera *Trochomeria*, *Blastania* Kotschy & Peyr. (syn. *Ctenolepis* Hook.f.), and *Benincasa* Savi (Schaefer et al. 2009; Schaefer and Renner 2011). However, these analyses only included one representative per genus, so could not elucidate the evolution and historical biogeography within *Dactyliandra*.

Here, we use a comprehensive sample of *Dactyliandra* and presumed relatives to test in a phylogenetic framework the hypotheses that 1) *Dactyliandra* is monophyletic, and 2) populations in India/Pakistan, East Africa, and Southwest Africa are three genetically and morphologically distinct entities and remainders of a former widespread ancestor, whose range covered the entire Saharo-Sindian desert belt region.

MATERIALS AND METHODS

Taxon Sampling—For the molecular phylogenetic analyses, we included seven accessions of *Trochomeria* and 15 accessions representing the three or four *Dactyliandra* species: ten specimens of *D. welwitschii*/*D. luederitziana*, four of them from Namibia, and three from India and Angola respectively, and we downloaded sequences for an additional Namibian sample from GenBank. For *D. stefanii* and *D. nigrescens*, we sequenced two specimens each, all of East African origin. For the presumed sister genus *Trochomeria*, we included the following four species in our phylogenetic analyses: *T. debilis* Benth. & Hook.f. (one specimen), *T. macrocarpa* Harv. (three specimens), *T. polymorpha* Cogn. (two specimens), and *T. sagittata* Benth. & Hook.f. (one specimen). Finally, we added five samples of the genera *Blastania* and *Benincasa* as outgroups based on the results of earlier family-wide analyses



FIG. 1. *Dactyliandra welwitschii* Namibia, Farm Kyffhauser. A. Habit; note simple tendrils and 5-lobed leaf. B. Male flower and ciliate bracts; note glandular hairy petal surface. C. Unripe green fruits. D. Mature pink fruits. Scale bars = 5 mm. (Photographer A. Dreyer).

(Schaefer et al. 2009, Schaefer and Renner 2011). Appendix 1 provides voucher information and GenBank numbers for all included sequences.

For the morphological comparisons and development of the determination key, we studied 115 specimens at the herbarium of Royal Botanical Gardens Kew (K); for the genus *Dactyliandra*, we studied 52 specimens of *D. welwitschii*/*D. luederitziana*, eight specimens of *D. stefaninii*, and eight specimens of *D. nigrescens*; 15 specimens of *Blastania cerasiformis*

(Stocks) A. Meeuse, 26 of *Trochomeria macrocarpa* (Sond.) Hook.f., five of *T. polymorpha* Cogn., and one of *T. debilis* Hook.f. (for specimen details see appendix). Further specimens from the herbarium of the Botanische Staatssammlung Munich (M) were studied to see if morphological variation was within the range of variation of the vouchers in K. All measurements were taken from dry herbarium specimens.

Scans of type material of all *Dactyliandra* species can be accessed in the Global plants database of JSTOR using the following links:

<http://plants.jstor.org/compilation/Dactyliandra.welwitschii>

<http://plants.jstor.org/compilation/Dactyliandra.nigrescens>

<http://plants.jstor.org/compilation/Dactyliandra.stefaninii>

DNA Extraction and PCR—DNA extraction followed standard procedures described in Kocyan et al. (2007). Polymerase chain reactions (PCR) were performed using two different premixed reaction kits: a) the Nova Taq™ PCR Master Mix (Merck) and b) the KAPA2G™ Fast 2x ReadyMix (Kapa Biosystems Inc.). We amplified the nuclear ribosomal internal transcribed spacer (ITS) region using the primers of Douzery et al. (1999), and from the plastid genome the *rbcL* and *matK* genes, the *rpl20-rps12* spacer, the *trnL* intron and *trnL-trnF* spacer with the primers listed in Kocyan et al. (2007), and the *trnH-psbA* spacer with the primers of Sang et al. (1997). The PCR products were cleaned with the ExoSAP-IT® enzyme mix. Then we sent the cleaned PCR products premixed with sequencing primer to a private company (GATC Biotech AG, Konstanz, Germany) for Sanger sequencing. Each PCR product was sequenced in two directions and the sequences edited and assembled using Geneious v. 6.0 (Biomatters Ltd., Auckland, New Zealand). Eighty-nine sequences were generated for this study. An additional 17 sequences were downloaded from GenBank (www.ncbi.nlm.nih.gov/genbank/), most from our previous family-wide analyses (Kocyan et al. 2007, Schaefer et al. 2009). Appendix 1 lists the relevant taxonomic names with authors, vouchers, geographic origin, and GenBank accession numbers (KU289638–KU289736).

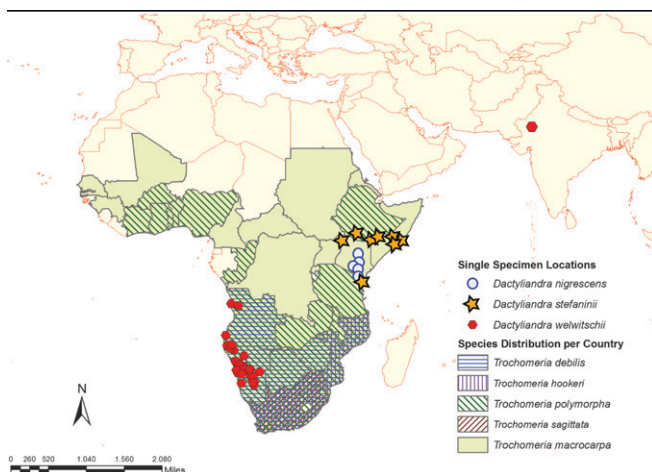


FIG. 2. Distribution map showing the natural ranges of the species of *Dactyliandra* and *Trochomeria* based on all label information of all herbarium material seen.

Sequence Alignment and Phylogenetic Analyses—Sequences were aligned using the Geneious alignment algorithm implemented in Geneious. Unambiguous gaps in the ITS, *trnH-psbA*, and *rpl20-rps12* alignments were coded manually as binary characters following Simmons & Ochoterena (2000) and added as additional columns to the three alignments. Maximum likelihood (ML) analyses (and non-parametric bootstrap searches with the fast-bootstrap algorithm) were performed using RAxML-VI-HPC (Stamatakis et al. 2008) on the CIPRES science gateway (Miller et al. 2010). Based on the Akaike Information Criterion (Akaike, 1974) as implemented in jModeltest (Posada 2008) we selected the GTR + G model (six general time-reversible substitution rates, assuming gamma rate heterogeneity), with model parameters estimated over the duration of specified runs. Analyses in RAxML were first run on all six alignments (including the coded gap columns) independently. We then tested congruence of the five plastid regions and the ITS data using the Partition Homogeneity test in PAUP* version 4.0a149 (Swofford 2002) and by manual comparison of the individual topologies. No incongruence was detected, so all sequenced regions were concatenated into a single final alignment.

Divergence Time Estimation—Divergence times were estimated using the Bayesian relaxed clock approach implemented in BEAST version 1.8.2 (Drummond and Rambaut 2007). Following the BEAST manual (Drummond and Rambaut 2007), we modified our final combined sequence dataset slightly: we merged identical sequences and deleted the coded indel columns from the matrix. Three clades were defined a priori based on the results of our ML analyses and previously published phylogenies (Kocyan et al. 2007; Schaefer et al. 2009; Schaefer and Renner 2011): (a) *Benincasa*, (b) *Blastania*, (c) *Blastania* + *Trochomeria* + *Dactyliandra*. In the absence of fossils for our clade of interest, we followed a secondary calibration approach and constrained divergence times for three nodes and the root of our tree using the results of a previous family-wide analysis (Schaefer et al. 2009). Specifically, we set the split *Benincasa hispida* (Thunb.) Cogn. - *B. fistulosa* (Stocks) H.Schaefer & S.S. Renner (syn. *Praecitrullus fistulosus* (Stocks) Pangalo) to 5 ± 2 Ma (million years ago), the split *Blastania cerasiformis* - *Bl. lucorum* to 7 ± 3 Ma, the split *Blastania* vs. *Trochomeria* plus *Dactyliandra* to 10 ± 3 Ma, and the root of our tree (*Benincasa* vs. all other taxa) to 13 ± 3 Ma, all with a normal prior distribution. Searches used a Yule tree prior, the GTR + G (general time reversible plus gamma) substitution model, and 50 million Markov chain Monte Carlo (MCMC) generations, sampling every 1,000th generation. Tracer version 1.5 (Rambaut and Drummond 2009) was used to check that effective sampling sizes had all reached > 200 , suggesting convergence of the chains. TreeAnnotator, part of the BEAST package, was then used to create a maximum clade credibility tree after removal of a burn-in of 10,000 trees from each of the four independent BEAST searches. The resulting chronogram was visualized using FigTree v.1.4.0. (<http://tree.bio.ed.ac.uk/software/figtree/>).

Biogeographic Analysis—To estimate the ancestral range of the lineage and reconstruct the origin of the Thar desert population of *Dactyliandra*, we coded species' geographic ranges as an unordered multistate character, using the following character states: i) Asia, ii) Namibia, iii) Angola, iv) East Africa, and v) Madagascar. We then imported the highest likelihood tree with branch lengths into Mesquite 3.04 (Maddison and Maddison 2009) and used the Markov k-state one-parameter model (Lewis 2001), which assumes a single rate for all character state transitions to infer the probabilities of shifts between biogeographic regions.

RESULTS

Morphology—The two East African species *Dactyliandra nigrescens* and *D. stefaninii* differ from the remaining species in the genus in their sexual system (both dioecious) and in anther morphology with S-shaped thecae instead of hippocrepiform thecae. None of the studied leaf or flower characters allowed to consistently separate Indian *D. welwitschii* from Angolan *D. welwitschii* or from Namibian material labelled as *D. luederitziana*. The leaf characters given by Cogniaux (1916) were found to be inadequate to separate the two species described from Southwest Africa, so we treat *D. luederitziana* in the following as a synonym of *D. welwitschii*.

Sequence Analysis of the Nuclear ITS Region—The ITS alignment includes 19 sequences with a total length of 817 aligned nucleotides plus 11 coded gaps. *Dactyliandra* is represented by five *D. welwitschii* accessions from Namibia,

three from Angola, and three from India. Furthermore, there is one sequence of *D. stefaninii* from Ethiopia and three *Trochomeria* plus three *Blastania* sequences. Unfortunately, all attempts to amplify and sequence ITS for the remaining samples failed. The *D. stefaninii* sequence is very similar to the sequence of *Trochomeria macrocarpa* from Burkina Faso (two nucleotides different) but differs considerably from all *D. welwitschii* sequences. The Namibian *D. welwitschii* samples are represented by two ribotypes differing in three positions. Among the three Angolan samples, we also found two ribotypes differing in nine positions. All three Indian samples have identical ITS sequences, which are very similar to one of the Angolan ribotypes (*Carriso and Sousa 3/8*) differing only in the number of repeats in a poly guanine zone at position 184 of our alignment (six repeats instead of five).

Sequence Analyses of the Plastid Regions—Among the five chloroplast DNA regions amplification success was highest for the *trnH-psbA* spacer region, where our alignment includes 18 sequences of a total aligned length of 266 nucleotides plus four coded gaps. The four East African *Dactyliandra* sequences (one from *D. nigrescens*, three from *D. stefaninii*) are all quite different from *D. welwitschii* (up to six differences) and appear most similar to *Trochomeria debilis* and *T. sagittata*. For *D. welwitschii*, we obtained four sequences from Namibian samples, one from Angola and three from the Indian material. All Namibian sequences are identical and differ from the Angolan sequence in two positions. The three Indian samples represent two different haplotypes, differing from the Angolan and Namibian sequences in one to three positions.

For *rbcL*, our alignment includes 16 sequences with a total length of 1,375 nucleotides. We were unable to produce an *rbcL* sequence for any of the East African *Dactyliandra* samples, but for *D. welwitschii*, we obtained four sequences from Namibian material, two from Angolan samples and two for India (the latter only ca. 800 nucleotides long). These sequences are all identical except for one variable site (position 844), where one Angolan and one Namibian accession share a cytosine, whereas the two Indian accessions share a thymine with the second Angolan sequence (*Carriso and Sousa 3/8*).

Our *matK* alignment includes 15 sequences of a total aligned length of 1,143 nucleotides. Again, we had no amplification success for the East African samples but managed to get seven *D. welwitschii* sequences, three for Namibia and two each for Angola and India. The Namibian sequences are identical and differ from the Angolan and Indian sequences in three positions. Of the two Angolan sequences, one (*Carriso and Sousa 3/8*) is identical to the two Indian sequences, the second differs in one position.

For the *trnL* intron and *trnL-trnF* spacer region our alignment contains 19 sequences with a total aligned length of 957 nucleotides. One *D. stefaninii* sequence from Ethiopia was obtained and appears most similar to *Trochomeria macrocarpa* sequences but very different from *D. welwitschii*. For the latter, five sequences of Namibian material are identical and differ from the one Angolan and three Indian sequences in just one position (581), where the latter have a guanine instead of a thymine.

Finally, the *rpl20-rps12* spacer alignment contains 15 sequences with a total aligned length of 745 nucleotides plus five coded gaps. The sequences for *D. nigrescens* and *D. stefaninii* are again more similar to *Trochomeria* sequences than to *D. welwitschii*. The five Namibian *D. welwitschii* sequences are identical. The one Angolan sequence is identical to the two

from India and both differ from the Namibian sequences in six positions.

Phylogeny Inferences—The ML tree for the ITS alignment (Fig. 3) shows a highly supported *D. welwitschii* clade, with two Angolan samples branching first and then a sister relationship of a highly supported Namibian clade with a third highly supported clade of the Indian samples plus one from Angola. The genus *Trochomeria* does not appear to be monophyletic but rather a grade with *T. polymorpha* branching off first, then followed by a clade with *T. sagittata* and *T. macrocarpa* from Burkina Faso, which is sister to the only East African *Dactyliandra* for which we obtained an ITS sequence (*D. stefanii* from Ethiopia). *Blastania* is sister to all *Trochomeria* and *Dactyliandra* samples.

For the combined plastid alignment, the ML phylogeny (Fig. 4) is similar in topology to the ITS tree. *Dactyliandra* is monophyletic when the East African species are excluded. One Angolan sample groups with the Indian samples and is sister to a well-supported Namibian clade. *Trochomeria* is not well-

supported as a clade and two East African *Dactyliandra* samples seem to group as a separate clade outside *Trochomeria*. *Blastania* is again sister to all *Trochomeria* and *Dactyliandra* samples.

Finally, the analysis of the combined ITS and plastid alignments resulted in a phylogeny where *Blastania* is sister to a *D. welwitschii* clade (Angola plus India, Namibia) plus *Trochomeria* with inclusion of *D. stefanii* and *D. nigrescens* (Fig. 5). However, the bootstrap support for the *Trochomeria* clade is low.

Chronogram—The divergence time analysis resulted in a chronogram with a well-supported topology identical to the combined ML tree (Fig. 6). The 95% HPD (highest posterior density) for the divergence time estimate for the split between *D. welwitschii* and the *Trochomeria* clade is 10.8–6.1 Ma (best estimate 8.5 Ma), for the crown node of *D. welwitschii* it is 6.4–2.4 Ma (best estimate 4.3 Ma), and for the split between the Namibian and the Angolan/Indian clade it is 4.6–1.5 Ma (best estimate 3 Ma). The age of the Indian samples must be younger than the split between the

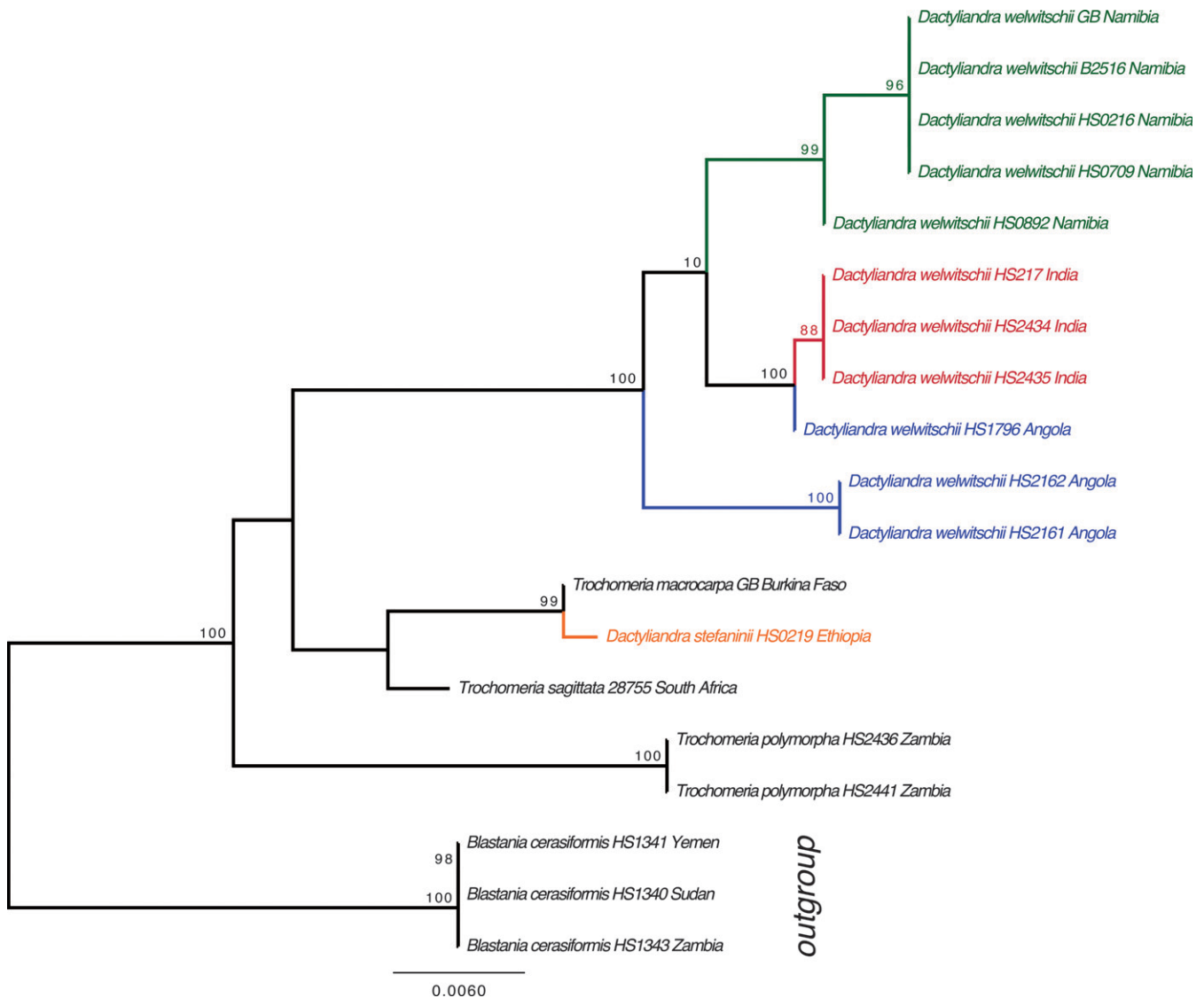


FIG. 3. Maximum likelihood (ML) tree for *Dactyliandra* and relatives based on 817 nucleotides of the nuclear rDNA ITS 1, the 5.8S gene, and ITS 2. ML bootstrap support $\geq 50\%$ given at the nodes. Native range indicated by colour: red = India, green = Namibia, blue = Angola, orange/yellow = East Africa, black = other.

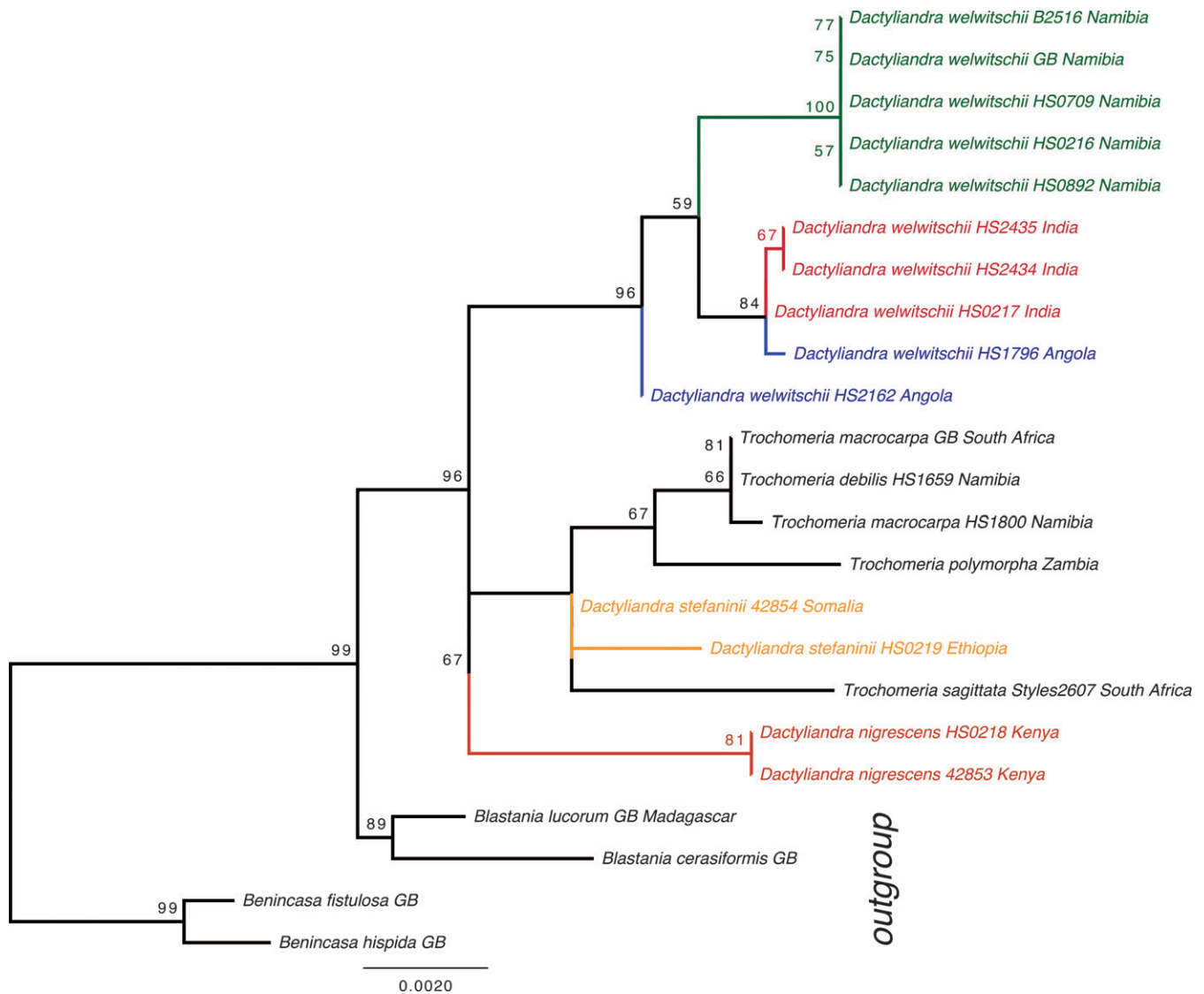


FIG. 4. ML tree for five plastid DNA regions combined (4495 nucleotides). ML bootstrap support $\geq 50\%$ given at the nodes. Native range indicated by colour: red = India, green = Namibia, blue = Angola, orange/yellow = East Africa, black = other.

Angolan specimen *Carrisso & Sousa 3/8* (HS1796) and the three Indian samples estimated to 1.7–0.16 Ma.

Biogeography—The geographic origin of the *Dactyliandra*/*Trochomeria* clade is estimated to be in East Africa (Fig. 7). The ancestral range of *D. welwitschii* is reconstructed as Angolan, from where the plants colonized both Namibia and India.

DISCUSSION

Taxonomy—The morphological and molecular data both indicate that *Dactyliandra welwitschii* is monophyletic but not the genus *Dactyliandra* as a whole. The two East African species that seemed to be a possible link between the Namib and Thar desert populations (Jeffrey 1965) are in fact better placed in the genus *Trochomeria* as *T. stefaninii* (Chiov.) C. Jeffrey and *T. nigrescens* (C. Jeffrey) H. Schaeff., a new combination for the latter is formalized in our key below. Our results support maintaining two different species in East Africa, even though their precise relationship and position within *Trochomeria* could not be definitely resolved in our

analysis, due to the poor amplification success with the old East African material and incomplete sampling of *Trochomeria*. Fieldwork in East Africa for collection of ecological and morphological data and fresh leaf material for good quality DNA is needed to obtain a more definite answer for this question. We find no support for a split of the Namib population in an Angolan *D. welwitschii* and a Namibian *D. luederitziana* as suggested by Cogniaux (1916).

Biogeography—Our results reject the hypothesis of a widespread ancestor and three long isolated refugial areas for the genus *Dactyliandra*. Instead, the most likely explanation for the striking 8000 km disjunction between the Namib region and Rajasthan seems to be a recent introduction of *D. welwitschii* from Angola to Northern India or Pakistan. We acknowledge that our divergence time estimate seems a bit too old to be explained by human-mediated transport. However, molecular clock estimates, especially those based on secondary calibrations, are not very precise. Moreover, our sampling of *Dactyliandra* from Angola is very small, so we have probably not found the closest relatives of the

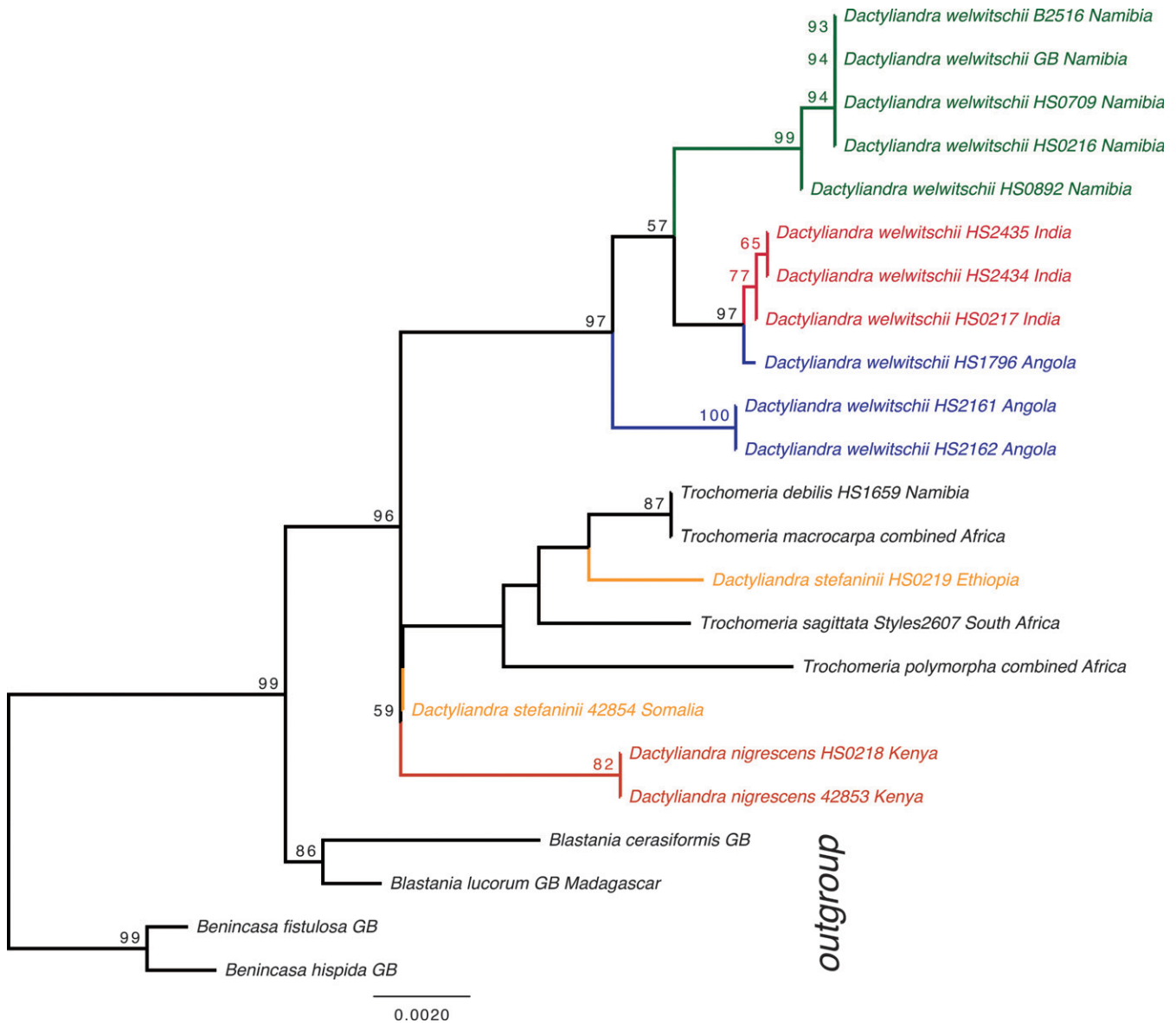


FIG. 5. ML tree for ITS plus five plastid DNA regions combined (5323 nucleotides). ML bootstrap support $\geq 50\%$ given at the nodes. Native range indicated by colour: red = India, green = Namibia, blue = Angola, orange/yellow = East Africa, black = other.

Indian plants. Adding them would reduce the divergence time estimate even further. In any case, a recent divergence of one million years or less does not fit to the idea of an ancient disjunction.

The results of the ancestral range estimation clearly show that an Angolan origin of the *Dactyliandra* population in India/Pakistan is most likely (Fig. 7). When searching for possible connections between Angola and Rajasthan, we found no evidence for bird dispersal. The small pink berry fruit (Fig. 1D) is probably eaten by birds but at least today, there are no bird migration routes from Angola to Rajasthan. External transport like in the cucurbit genus *Sicyos* (Sebastian et al. 2012) seems impossible because of the lack of any structures on the seed surface that would attach the seeds to legs or feathers of a bird. Regarding possible human transport, there seem to be no links between the two regions today. However, Shah et al. (2011) analysed in a recent study the origin of the Siddi people, a group of African origin today

living in parts of India and Pakistan, including the Gujarat region, where *Dactyliandra* is found. Shah and colleagues conclude that the Siddi people have been brought to India as slaves mainly by the Portuguese from their former African colonies, which includes Angola. However, the earliest records of Siddi people in India are much older and date to 1100 AD (Shah et al. 2011 and references therein). We therefore suggest as one possible explanation for the disjunction of *D. welwitschii* an introduction with African slaves from Angola to Gujarat. A similar human-mediated dispersal scenario has been suggested to explain the tropical America – West Africa disjunction in *Melothria sphaerocarpa* (Cogn.) H. Schaeff. & S.S. Renner (previously known as *Cucumeropsis mannii* Naudin), which might have been introduced from Brazil to West Africa during the times of the slave trade (Schaefer and Renner 2010). We searched for ethnobotanical evidence for medicinal usage of *D. welwitschii* in Namibia and Angola, and also in the Thar region. All we found was

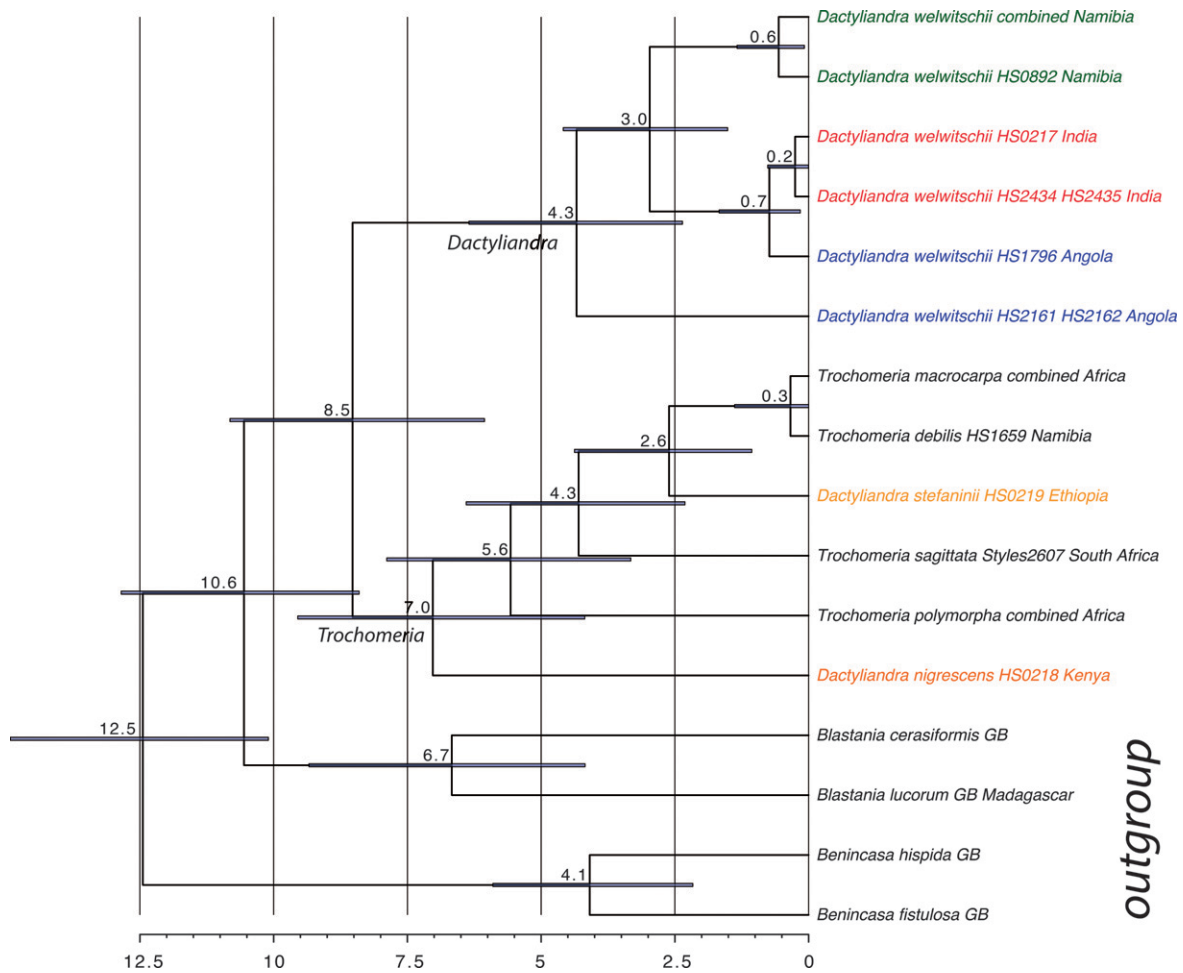


FIG. 6. Chronogram for *Dactyliandra* and relatives based on the combined nrITS and plastid sequences estimated using BEAST version 1.8.2 (Drummond and Rambaut 2007). Scale bar in million years before present, numbers at the nodes are best age estimates, blue bars indicate the 95% CI ranges.

that the species is listed in a register of Indian medicinal plants (Tandon and Sharma 2009). However, no actual usage is indicated in this register; only the high content of linoleic acid in its seeds is mentioned. This questions the assumed medicinal importance, but the knowledge about its medicinal properties could have been lost or *Dactyliandra* could have been replaced by more powerful drugs. What we know about the species habitat in India would also fit to a history of active introduction followed by escape from cultivation: in a recent field survey, Joshi et al. (2013) found only 38 individuals in four places in “agricultural hedges covered by dried thorny twigs and branches” on sand. They did not find *D. welwitschii* in natural habitats and this is similar to earlier reports from hedges around cultivated areas (Bhandari 1978, p. 154). Taken together with the low genetic diversity in the Indian population compared to the African plants, all this indicates that *D. welwitschii* is not indigenous to the Thar region and the striking disjunction is just the result of human activities. We cannot provide hard evidence that the slave trade is responsible for introduction of *Dactyliandra* to India, but based on our results, the hypothesis cannot be rejected either. More fieldwork to gather additional plant material and also direct ethnobotanical evidence from both Southwest Africa and the Thar region is needed to definitely answer the question.

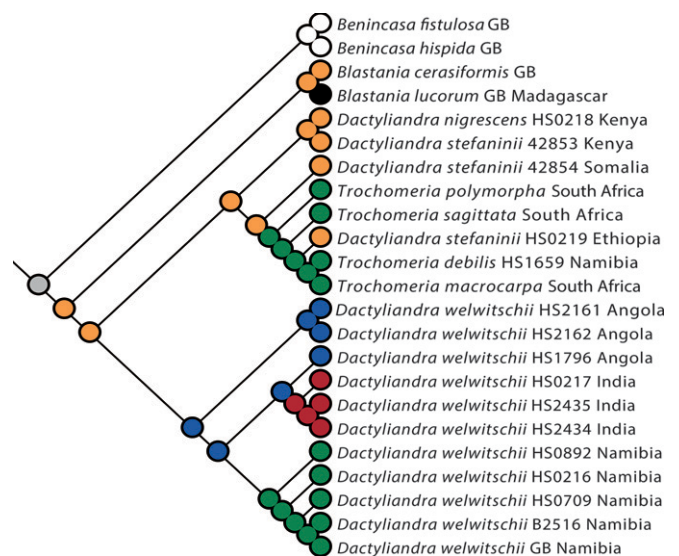


FIG. 7. Ancestral range reconstruction for *Dactyliandra* and relatives based on the combined nrITS and plastid sequences estimated using Mesquite version 3.0.4 (Maddison and Maddison 2009). Regions of origin are color-coded: India = red, Namibia/South Africa = green, Angola = blue, East Africa = orange, Madagascar = black, ambiguous = grey, not coded (outgroups) = white.

KEY TO SPECIES OF *DACTYLIANDRA*, *TROCHOMERIA*, AND *BLASTANIA*

This determination key is based on our own measurements plus literature data (Jeffrey 1965, 1967, 1985). It includes all species of *Dactyliandra*, all species of *Blastania* and all accepted species of *Trochomeria* except the poorly known *T. baumiana* Gilg, *T. teixeirae* R. Fern & A. Fern, and *T. wyleyana* Benth. & Hook.f. for which we could not find sufficient material. For the genus *Blastania* (usually referred to as *Ctenolepis*), we here follow Kartesz & Gandhi (1994), who concluded that *Blastania* (Stocks) Kotschy & Peyr. has priority because it was published in July 1867 (in Kotschy and Peyritsch's *Plantae Tinneanae*, 1867) while *Ctenolepis* (Stocks) Hook.f. was published in September 1867 (Bentham and Hooker's *Genera Plantarum*, 1867).

1. Plant monoecious, with male and female flowers on the same individual. 2
2. Bract margin dentate to shortly ciliate, the cilia length not exceeding half the bract's diameter. *Dactyliandra welwitschii* Hook.f.
2. Bract margin long ciliate, the cilia at least as long as the bract diameter. 3
 3. Male and female inflorescences very short and concealed by bract (India and Sri Lanka). *Blastania garcinii* (Burm.f.) Cogn.
 3. Inflorescences longer, with pedicels of female flowers and peduncles of male racemes ≥ 7 mm, inflorescence not concealed by bract (subtropical and tropical Africa, India and Pakistan). *Blastania cerasiformis* (Stocks) A.Meeuse
1. Plant dioecious, with male and female flowers on separate plants. 4
4. Species confined to Madagascar. ***Blastania lucorum*** (Keraudren) H.Schaeef. comb. nov. (basonym: *Zombitsia lucorum* Keraudren, *Adansonia* ser. 2, 3:167. 1963)
4. Species from the African mainland. 5
 5. Tendrils absent. *Trochomeria polymorpha* Cogn.
 5. Tendrils present. 6
 6. Stipuliform bract absent. 7
 7. Male receptacle tube \pm cylindrical, ≥ 13 mm long. *Trochomeria macrocarpa* (Sond.) Hook.f.
 7. Male receptacle tube \pm campanulate, ≤ 4 mm long. 8
 8. Leaf blade broadly ovate-reniform, palmately 3-lobed, central lobe largest, lobes obovate-rhombic. *Trochomeria stefanii* (Chiov.) C. Jeffrey
 8. Leaf blade variable in outline. Lobes always deeply sagittate and acute, leaf length and breadth and number of lobes variable. *Trochomeria sagittata* Cogn.
 6. Stipuliform bract present (at least in a few axils). 9
 9. Male receptacle tube \pm cylindrical, ≥ 10 mm long. 10
 10. Corolla lobes rotate, angled, not strongly recurved and not exceeding half the receptacle tube length (Southern Africa). *Trochomeria debilis* Hook.f.
 10. Corolla lobes of mature flowers strongly recurved. 11
 11. Corolla lobes exceeding half the receptacle tube length (sub-Saharan Africa). *Trochomeria macrocarpa* (Sond.) Hook.f.
 11. Corolla lobes not exceeding half the receptacle tube length (Mozambique, South Africa, Swaziland). *Trochomeria hookeri* Harv.
 9. Male receptacle tube campanulate, ≤ 2.5 mm long. 12
 12. Rachis of raceme geniculate (zig-zag shaped). *Trochomeria stefanii* (Chiov.) C. Jeffrey
 12. Rachis not geniculate. 13
 13. Fruit globose, not beaked, testa distinctly pitted. *Trochomeria stefanii* (Chiov.) C. Jeffrey
 13. Fruit shortly beaked and testa smooth. ***Trochomeria nigrescens*** (C. Jeffrey) H. Schaeef. comb. nov. (basonym: *Dactyliandra nigrescens* C. Jeffrey, *Kew Bull.* 19: 221. 1965)

ACKNOWLEDGMENTS. We thank A. Dreyer, Farm Kyffhauser, Namibia for allowing us to use his photographs of *D. welwitschii*, S. Schepella for lab work, the curators of the K and M herbaria for allowing us to study their collections, and M. Romeiras for photographs and samples of LISC specimens. Arun Pandey thankfully acknowledges grant support from SERB-DST, New Delhi (#SR/SO/PS/116/2010).

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- APPENDIX 1. Species and specimens sequenced for this study, voucher specimen, geographic origin, and GenBank accession numbers for *rbcL*, *matK*, *psbA-trnH*, *trnL* intron and *trnL-F* spacer, *rpl20-rps12* spacer, and ITS1-5.8s-ITS2 respectively. An asterisk (*) indicates sequence for the subsequent region was not obtained. Herbarium acronyms follow the Index Herbariorum (Thiers [continuously updated]).
- Dactyliandra nigrescens* C. Jeffrey, DNA no. HS218, Kirrika 34 (K), Kenya, Isiolo, **, KU289713, *, KU289638, *, *Dactyliandra nigrescens* C. Jeffrey, DNA no. 42853, Stannard & Gilbert 1108-1111 (K), Kenya, Kitui District, **, KU289716, *, *, *, *Dactyliandra stefaninii* (Chiov.) C. Jeffrey, DNA no. 42854, Lavaranos & Carter 23311 (K), Somalia, Shabeellaha Dhexe, *, *, KU289715, *, *, *, *Dactyliandra stefaninii* (Chiov.) C. Jeffrey, DNA no. HS219, Gilbert & Jefford 4586 (K), Ethiopia, Sidamo, *, *, KU289714, KU289690, KU289652, KU289639, KU289678, *Dactyliandra welwitschii* Hook. f., DNA no. B2516, Seydel 796 (B), Namibia, Okongawa, KU289702, KU289731, KU289719, KU289691, KU289653, KU289640, KU289679, *Dactyliandra welwitschii* Hook. f., DNA no. HS216, Oliver, Muller, Steenkamp 6549 (K), Namibia, Weltevrede, *, *, KU289718, KU289692, KU289655, KU289641, KU289680, *Dactyliandra welwitschii* Hook. f., Giess 3664 (M), Namibia, Brandberg, 21°9'54.19"S, 14°39'39.15"E, DQ535750, DQ536669, *, DQ536810, DQ536545, HQ201973, *Dactyliandra welwitschii* Hook. f., DNA no. HS709, unvouchered, Namibia, KU289703, KU289732, KU289717, KU289693, KU289656, KU289642, KU289681, *Dactyliandra welwitschii* Hook. f., DNA no. HS892, Seydel 990 (US), Namibia, Karibib, KU289705, *, KU289720, KU289694, KU289657, KU289643, KU289682, *Dactyliandra welwitschii* Hook. f., DANN no. HS2434, Pandey s.n., India, Rajasthan, KU289707, KU289735, KU289723, KU289696, KU289659, KU289645, KU289687, *Dactyliandra welwitschii* Hook. f., DNA no. HS2435, Pandey 2201, India, Rajasthan, KU289708, KU289736, KU289724, KU289660, *, KU289688, *Dactyliandra welwitschii* Hook. f., DNA no. HS217, Bhandari 332 (K), India, Rajasthan, Jodhpur-Balsamand, *, *, KU289722, KU289695, KU289658, KU289644, KU289686, *Dactyliandra welwitschii* Hook. f., DNA no. HS1796, Carriso & Sousa 3/8 (M), Angola, Moçamedes [Namibe], Rio Muçungo, KU289706, KU289733, KU289721, KU289654, KU289646, KU289685, *Dactyliandra welwitschii* Hook. f., DNA no. HS2162, Menezes, Barroso & Sousa 4719 (LISC), Angola, Cunene, Curoza, KU289704, KU289734, *, *, KU289647, KU289684, *Dactyliandra welwitschii* Hook. f., DNA no. HS2161, Henriques 510 (LISC), Angola, Moçamedes, KU289709, *, *, *, KU289683.
- Outgroups: *Blastania cerasiformis* (Stocks) A. Meeuse, M. Wilkins 279, Zimbabwe, DQ535797, DQ536656, *, DQ536803, DQ648164, *, *Blastania cerasiformis* (Stocks) A. Meeuse, DNA no. HS1343, Kirk s.n. (GH), Zambia, *, *, KU289711, *, *, KU289672, *Blastania cerasiformis* (Stocks) A. Meeuse, DNA no. HS1340, Kotschy 205 (M), Sudan, *, *, *, *, KU289673, *Blastania cerasiformis* (Stocks) A. Meeuse, DNA no. HS1341, Schueinurth 557 (M), Yemen, *, *, *, *, KU289674, *Ctenolepis lucorum* (Keraudren) H. Schaefer & S.S. Renner, Phillipson 2541 (P), Madagascar, DQ501260, DQ491024, *, DQ501273, *, *, *Trochomeria debilis* Hook. f., DNA no. HS1659, Seydel 3043 (GH), Namibia, *, *, KU289725, KU289697, KU289661, *, *, *Trochomeria macrocarpa* (Sond.) Hook. f., DNA no. HS1800, Seydel 2512 (M), Namibia, *, *, *, KU289666, KU289650, *, *Trochomeria macrocarpa* (Sond.) Hook. f., Giess 13286 (M), Namibia, DQ535858, DQ536745, *, DQ536877, DQ536606, *, *Trochomeria macrocarpa* (Sond.) Hook. f., Achigan-Dako 06nia158 (GAT), Burkina Faso, Ouagadougou, *, *, *, *, AM981141, *Trochomeria polymorpha* (Welw.) Cogn., DNA no. HS2436, Schaefer HSC5 (TUM), Zambia, KU289700, KU289729, KU289727, KU289698, KU289668, KU289648, KU289675, *Trochomeria polymorpha* (Welw.) Cogn., DNA no. HS2441, Schaefer HSC10 (TUM), Zambia, KU289701, KU289730, KU289726, KU289699, KU289669, KU289649, KU289676, *Trochomeria sagittata* Cogn., DNA no. 28755, Styles 2607 (GH), Republic South Africa, Kwazulu-Natal, inland Durban, *, *, KU289728, KU289670, *, KU289677.
- APPENDIX 2. Representative specimens examined.
- Dactyliandra nigrescens* C. Jeffrey: KENYA. Isiolo, 4,500 ft. asl., Kirrika 34 (K). Kitui District, ca. 5 km NW of Mutomo, 850 m asl., Gillett 16958 (K). Kitui, 65 km, from Mutomo on Kibwezi rd., GATHERI, Mungai, Kanuri Kibui 79/161 A (K). Kitui District, 111 km from Garissa on main rd to Thika, 510 m asl., Stannard & Gilbert 1108-1111 (K). Voi distr. Voi Gare, W-Pipeline M 4.5, 1,600 ft asl., Tsavo National Park, East, Greenway & Kanuri 12797 (K). Kitui District, 25 m SSW of Kitui, 3,200 ft asl., Bogdan 5124 (K). Kitui District, ca. 5 km NW of Mutomo, 850 m asl., Gillett 16954 (K).
- Dactyliandra stefaninii* (Chiov.) C. Jeffrey: ETHIOPIA. Sidamo, Old Airfield, ca. 15 km NNE of Yavello, 1,700 m asl., Gilbert & Jefford 4586 (K). Sidamo, 32 km NE of Dolo, road to Bokol Mayo, 300 m asl., Gilbert, Sebsebe, Vollesen 8160 (K). KENYA. Kwale distr., Kaya Muhaka (Kaya Kambe), 30 m asl., Robertson & Luke 6294 (K). Mandera distr., Ramu-Banissa Rd, 10 km from the turning to Banissa, Gilbert & Thulin 1424 (K). Turkana prov., 10 km S of road junction to Kakuma on Lokitaug-Lodwar rd, by Lomuyenakwa river, 600 m asl., Carter & Stannard 204 (K). SOMALIA. Shabeellaha Dhexe, 179 km NE of Mogadishu on Road to Harardere, Lavaranos & Carter 23311 (K). Jalalaksi distr, 9 km S of Jalalaksi, 125 m asl., Kuchar 17585 (K). Hiiraan reg., Bulu Burti distr., at a Bridge 1.6 km N on hwy from Halgan. 190 m asl., Kuchar & Ahmed 15555 (K). Hiiraan reg., Bulu Burti distr., 6 km N of Buli Burti Bridge on hwy. 0.3 km W along outline-like track. 155 m asl., Kuchar 15440 (K).
- Dactyliandra welwitschii* Hook. f.: ANGOLA. Moçamedes, Rio Muçungo, Trepadeira, Carriso & Sousa 3/8 (M). Loanda, Gossweiler 309 (K). Loanda, Welwitsch 833 (K). Merro da Famba?, Mendes dos Santos 1160 (K). Southern Angola, Pearson 2641 (K). Cuanza Norte, Cacoba, Proximum flumen Cuanza, Gossweiler 8835 (K). 3.5 miles N of Ohopoho, De Winter & Leistner 5646 (K). INDIA. Rajasthan, Jodhpur-Balsamand, Bhandari 332 (K). NAMIBIA. Omaruru, Merxmüller & Giess 1577 (M). Outjo, 37 miles from Fransfontein on Road to the Brandberg, 900–1,200 m asl., De Winter 3121 (M). Reoboth, about 20 miles from Kalkrand on road to Rehboth (on the

main Windhoek-Mariental-road), 1,200–1,500 m asl., *De Winter* 3537 (M). Kaokoveld, 3.5 miles N. Ohopoho, slope of mountain with dolomite and calcereous conglomerate, *De Winter & Leistner* 5246 (M). Namibrand Karibib Okomitundu, ca. 1,400 m asl., *Seydel* 1275 (M). Gibeon, ridge below the Hardap dam, *Giess, Volk & Bleissner* 5597 (M). 8 miles West of Orowanjai Fountain on rd to Orupembe (Anabib), *De Winter & Leistner* 5645 (M). Kaokoveld, am Ufer des Kunene bei Otjinungua, *Giess* 8930 (M). Okahandja, Farm Erichsfelde, Padrand, *Bleissner* 114 (M). Omaruru, Brandberg, Tsisabschlucht, *Urschler s.n.* (M). Omaruru, Brandenberg, Tsisab-Valley mouth, black stony kopjes, *Nordenstam* 2469 (M). Omaruru, Brandenberg, Tsisab-Valley, below the white Lady, in the riverbed, *Nordenstam* 2516 (M). Farm Fahlwater: KAR 9. Unterhalb von Granitrücken. Grober Granitgrus. 2116 CD Okabandja, *Giess* 11704 (M). Berghang, Fraventzheim, *Leippert* 4630 (M). Outjo, Farm Winkelhaag (OU 286); dolomit mountain, lower slope, *Merxmüller & Giess* 30364 (M). Brandberg, Southeast side c. 5 miles South Tsisab gorge, *Giess* 3664 (M). Kaokoveld, gully 77 miles from Ohopoho on road to Anabib (Orupembe), long 1302, lat 1821, *Story* 5683 (M). Sandy soils on bank of Kunene, long 1226, lat 1715, *Story* 5795 (M). Gibeon, *Launert* 2285 (M). Gobabis, Farm Donnersberg, *Volk* 1685 (M). Oterhandja, Erichsfelde, *Volk* 1889 (M). Windhoek, Farm Otjisewa, *Kinges* 2484 (M). Farm Nudis bei Karibib,

Seydel 42 (M). Shwatorz? River, *Wettstein* 41 (M), Namaqualand, Neue Rad und westliches Shuashwahland, ca. 1,800 m asl., *Meusel* 805 (M). Outjo, Onava, North of Tiervlei, *Crawford FC03* (K). *Strohbach* 2437 (K). 2115DD Trekkopje (Grid reference), 10 km towards Okahandja from Karibib; locally abundant, creeping in grasses, *Kubirske* 66 (K). Karibib. *Seydel* 990 (K). Rehoboth, *Strey* 2178 (K). sandy soil on banks of Kunene, long 1226, lat 1715, *Story* 5795 (K). Rehoboth, *Acochs* 18160 (K). Kaokoveld, Ohopoho on road to Anabib (Orupembe), long 1302, lat 1821, *Story* 5683 (K). Between Rehoboth and Uhlenhorst, *Willmann* 459 (K). Kaokoveld, 8 miles west of Orowanjai Fountain on the Road to Orupembe (Anabib), *De Winter & Leistner* 5645 (K). Karibib 140 m E of Swakopmund on Kohmas highland road to Windhoek, *De Winter & Hardy* 7999 (K). Farm Haribes, 32 m from Mariental-Maltahöhe, *Tölken & Hardy* 646 (K). 2116 CD Okahandja (Grid ref.), Farm Fahlwater, KAR 9, *Giess* 11704 (K). Swakopmund, crossing of Omaruru river, N of Hentjes Bay, *Wanntrop* 246 (K). 1712 BA (Grid ref.), Kaokoveld, Otjomborombonga on Kunene River, 360 m asl., *Leistner, Oliver, Steenkamp, Vorster* 114 (K). 2415B (Grid ref), Weltevrede, NE of Sossusvlei, *Oliver, Muller, Steenkamp* 6549 (K). 1613 CD (grid ref.), Kaokoveld, 6 km e of epupa falls, 620 m asl., *Leistner, Oliver, Steenkamp, Vorster* 269 (K). 2215 CD, Bloedkoppie, just w of Tinkas in Namib desert park, *Oliver, Muller, Steenkamp* 6592 (K). Okahnja, 1,300 m asl., *Dinter* (K).