

Largest on earth: Discovery of a new type of fairy circle in Angola supports a termite origin

NORBERT JÜRGENS,¹ FELICITAS GUNTER,¹ JENS OLDELAND,¹ ALEXANDER GROENGROEFT,² JOH R. HENSCHEL,^{3,5} IMKE ONCKEN¹ and MIKE D. PICKER⁴

¹Institute of Plant Sciences and Microbiology, Unit Biodiversity, Evolution and Ecology (BEE), University of Hamburg, Hamburg, Germany, ²Institute of Soil Science, University of Hamburg, Hamburg, Germany, ³SAEON Arid Lands Node, Kimberley, South Africa, ⁴Department of Biological Sciences, University of Cape Town, Cape Town, South Africa and ⁵Centre for Environmental Management, University of the Free State, Bloemfontein, South Africa

Abstract. 1. Circular bare patches occur in high numbers among the vegetation of the Namib Desert margin. There is an ongoing scientific debate on the origin of these so-called “fairy circles” (FCs). One of the most frequently discussed hypotheses regards the bare patches to be the result of localised herbivory by sand termites of the genus *Psammotermes* (family Rhinotermitidae).

2. In all earlier publications, the fairy circles of the Namib Desert region within their entire range from Angola through Namibia to South Africa were, in principle, regarded to be of one type, albeit increasing in size towards the north. Here we present evidence that at -16.23° latitude there is an abrupt discontinuity which separates the FCs on either side from each other.

3. South of this discontinuity all studied FCs share the properties of the previously described fairy circles in Namibia and South Africa, especially the presence of *Psammotermes* termites.

4. In contrast, north of -16.23°S the FCs are much larger and are caused by a different and undescribed termite species, most closely related to the harvester termite genus *Microhodotermes* (family Hodotermitidae). The two sets of fairy circles differ in a specific set of morphological features, associated termites, and soil parameters.

5. The observed juxtaposition of the newly discovered large structures caused by a hodotermitid termite and the *Psammotermes* FCs caused by a rhinotermitid species is interpreted as an interesting example of convergent evolution resulting in similar ecological structures.

Key words. Angola, termite, Namib, fairy circle, heuweltjie, Hodotermitidae.

Introduction

Namib fairy circles (FCs) are circular bare patches in semi-desert grassland that occur at the eastern margin of the Namib Desert. Fairy circles often occur in large numbers, most commonly in sandy soils, often possess circular belts of different vegetation, and have increased soil moisture underneath the bare patch (BP) (Van Rooyen *et al.*, 2004).

Correspondence: Norbert Jürgens, University of Hamburg, Institute of Plant Science and Microbiology, Research Unit Biodiversity, Evolution & Ecology (BEE) of Plants, Ohnhorststr. 18, 22609 Hamburg, Germany. E-mail: norbert.juergens@uni-hamburg.de

At present, two primary alternative hypotheses explain the fairy circles either as engineered ecosystems caused by localised herbivory of the termite *Psammotermes allocerus* Silvestri, 1908 (Juergens, 2013; Vlieghe *et al.*, 2015; Juergens *et al.*, 2015) or as a consequence of competition for scarce resources among plants (Cramer & Barger, 2013; Getzin *et al.*, 2015a,b). Additional hypotheses consider geogenic gases as the causative agent (Naudé *et al.*, 2011), or they interpret the BPs as a consequence of the earlier presence of toxic *Euphorbia* plants (Theron, 1979; Meyer *et al.*, 2015). Similar structures—although with partly cemented soils—have been described from more humid environments in Australia, and again they are either interpreted

as caused by *Drepanotermes Silvestri* termites (Watson & Gay, 1970; Watson *et al.*, 1973; Walsh *et al.*, 2016) or as an effect of self-organization processes among plants alone (Getzin *et al.*, 2016, 2019). Here, we focus exclusively on the fairy circles at the margin of the Namib Desert in southern Africa.

The presence of FCs in Angola had already been alluded to Moll, (1994), without, however, adding any information as to their nature or location. The first ground-truthing of these FCs in Angola was undertaken by the first author during fieldwork in the Iona National Park and near Moçâmedes in 2007, followed by field assessments and mapping of the giant bare circles near Baba and Chamune, in 2009 (Jürgens, 2013).

The Angolan FCs are also mentioned in subsequent publications (e.g. Cramer & Barger, 2013). However, until now, the morphology, ecology, biology, and origin of these northernmost fairy circles remain unknown. Here we examine these FCs using field observations, laboratory analyses, and phylogenetic studies.

Results

North of 16.23°S in SW Angola the FCs at first glance seem to be a continuation of the often-described Namib FCs, known from the Namib Desert margin further south in South Africa, Namibia, and the Iona National Park in SW Angola. Like these, the northernmost FCs also form roughly circular BPs within the desert margin grassland. They often occur in large numbers and form regular hexagonal patterns. The properties of these northernmost FCs follow the general pattern of increasing in diameter with decreasing latitude, running along the 100 mm MAP isohyet.

However, a closer examination reveals that these northernmost FCs form a separate set which share several striking differences. In the following, we describe these northernmost Namib fairy circles as a separate entity, preliminarily named “Baba FCs”, after the type locality right next to the coastal village Baba.

Biogeography

The FCs south of 16.23°S share the features which during the past two decades have been published as fairy circles of the Namib Desert, and they are closely associated with the termite *Psammotermes allocerus*. As will be shown in detail in the following, FCs north of 16.23°S (a) are not associated with *Psammotermes* termites but with a different termite family and (b) show several specific structural and environmental features. The more northern type of FC (in the following called “Baba FC”) is endemic to the coastal lowlands of the Namibé Province of SW Angola. The known range has an extension of 220 km in N–S and 45 km in W–E orientation (Fig. 1a). The Baba FCs were first found and studied at a coastal plateau near the village Baba, 35 km N of Moçâmedes. Additional populations were found along the coastal area of the Namibé Province, between just S of the Carunjamba River near Lucira (–13.99°) and just NE of Namibé (–15.04°). We studied FCs in-depth at Carunjamba, Chapeu Armado, Baba (referred to as Moscas by Jürgens, 2013) and Pipa. All these locations are characterised

by FC populations limited to small areas of only 10 km² or less. Further inland there is a large sand sheet with an area close to 200 km² north of the Rio Giraul (Fig. S3, study sites 2, 3 and 4). Further east and north of Caraculo and especially south of the rocky area which accompanies the Rio Giraul and Rio Bero, there are again large sand sheets with Baba FCs in the landscapes up to more than 70 km from the coast.

Most of the Baba FC locations comprise sand-covered plains or plateaus. Near the Atlantic coast, steep erosion cliffs indicate that those Baba FC landscapes are relicts of older geological formations that shrank in extent.

Baba fairy circle morphology

- (1) *Diameter*: The large diameter of Baba FCs (measured as the largest distance between the innermost parts of the first plants on either side) differs significantly from Namib FCs which occur further south. At Baba, the mean diameter of 164 FCs was 24.0 m (SD: 9.34, max: 53.8 m), which is significantly different from 164 FCs from the adjacent Iona National Park, with a mean diameter of 11.6 m (SD: 2.95, max: 27.3 m), ($t = 16.272$, $df = 195.28$, p -value < 0.001 ; Fig. 1b, c, Fig. 2). Baba FCs are two to nine times larger than the Namibian FCs and at least three times larger than the “Australian FCs” (Getzin *et al.*, 2019). While Baba FCs are circular on even inland plains, they show elongated or elliptical shapes on sloping ground and in the linear dune-interdune topography near the coastline (Fig. 1b).
- (2) *FC microtopography*: The BP of Baba FCs is nearly flat and at almost the same level as the surrounding soil surface (Figs 3 and 4a). Sometimes a very slight deflation of 1–3 cm can be observed at the outer parts of the BP, compared to the level of the matrix vegetation (MT). Deeper depressions, as caused by stronger wind erosion in the Namib FCs further south, do not occur in Baba FCs.
- (3) *Termite nest*: In contrast to the generally flat morphology of the Baba FCs bare patch, there is a slight elevation of up to 10 cm above the surface level in the central area of the BP (Fig. 4a, b). These slightly elevated areas form part of the nest system of termites; they can be regarded as termite mounds. These shallow mounds cover 5–20% of the bare patch surface. Sometimes the slight elevation forms a single circular patch. Occasionally several lobes are scattered over the central parts of the bare patch (Figs 4a and 5a). When undisturbed, the uppermost layer (0–15 cm, sometimes 30 cm) comprises a powdery thixotropic flour-like, highly saline sandy-silty material (Fig. 4b). The salt content is extreme, mainly based on Na⁺ and Cl⁻, but also including K⁺, SO₄²⁻, and NO₃⁻ (Table 1, Fig. 5c). Often the central mound area and the flat marginal areas differ in colour shades from white to ivory to grey to blackish. In most cases, the central nest area shows darker colour than the marginal areas (Fig. 4a). Sometimes, the material of the central nest can also be lighter in colour compared to the blackish-grey of the marginal parts of the bare patch when these are covered by a biological soil crust (Fig. 5a).

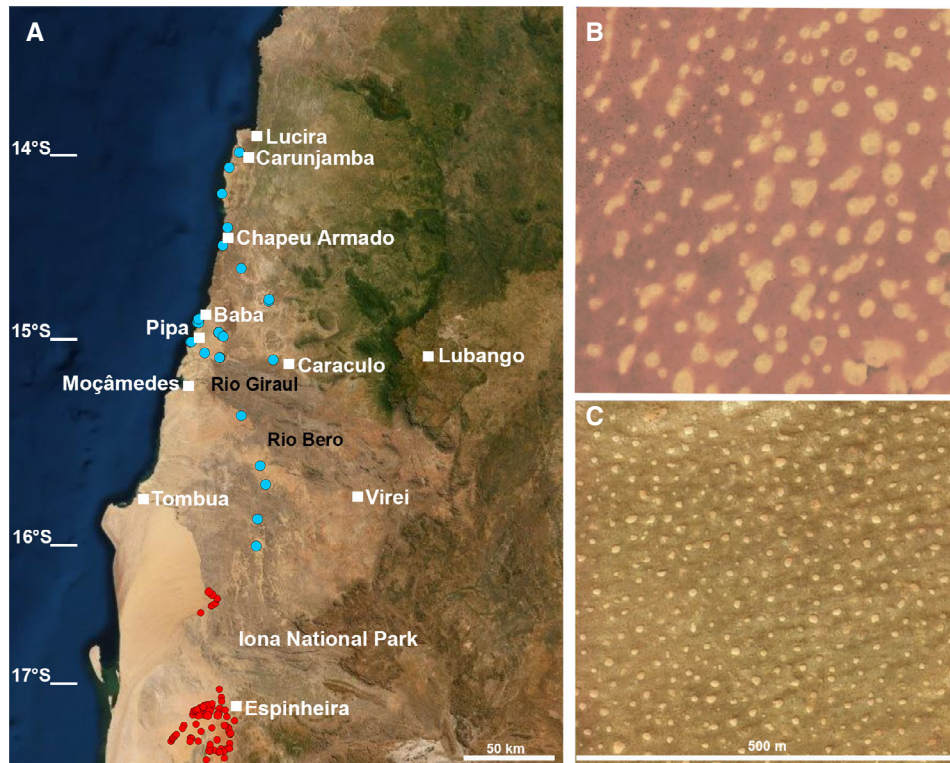


Fig. 1. Distribution of the Baba fairy circles (FCs) and *Psammotermes* FCs. (a) Geographical distribution of Baba FCs (blue circles), and *Psammotermes* FCs (red circles). (b and c) Size comparison of FCs at 25 ha plots (500 × 500 m) at Baba (b) and Iona National Park (c). Baba = -14.845952° , 12.222801° Google Earth 5/23/2010, Image C 2019 Maxar Technologies; Iona = -16.991851° , 12.194031° Google Earth 10/26/2018, Image C 2019 CNES/Airbus.) Scale: all edge lengths = 500 m. [Colour figure can be viewed at wileyonlinelibrary.com].

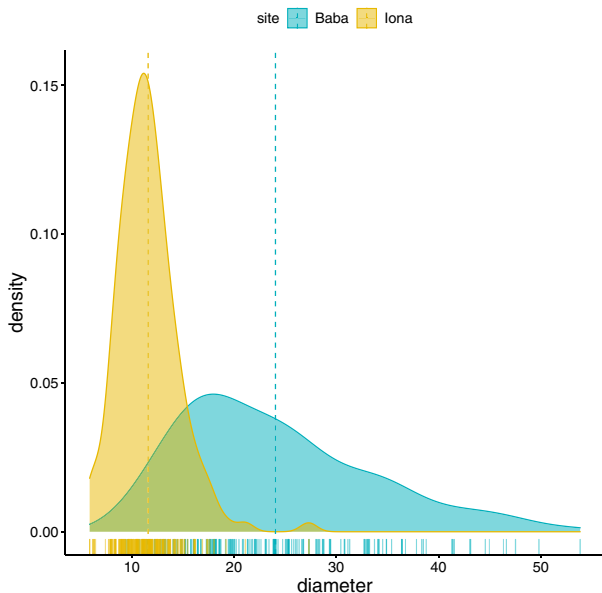


Fig. 2. Size distribution of Hodotermitidae bare patches at Baba and *Psammotermes* fairy circle diameters (m) at Iona (500 × 500 m). [Colour figure can be viewed at wileyonlinelibrary.com].

Underneath the powdery material, a cemented mineral soil contains flattened tunnels and chambers, the latter mostly of 2–5 cm diameter (Fig. 4c) which are partly filled with grass culms cut to a uniform length of ca 1 cm. The layer of cemented material extends to depths deeper than 120 cm (not excavated further). Some of the tunnels are filled with blackish organic material, which is similar in structure and colour to the frass of *M. viator* in the Karoo of South Africa (Coaton, 1958; Moore & Picker, 1991). Termites inhabit all these above-described structures. The soils of the matrix do not show this powdery flour-like, highly saline sandy-silty material and are less silty and less saline (Table 1).

- (4) Tunnel ports and soil dumps: As known for *Hodotermes mossambicus* and *Microhodotermes viator* there are numerous tunnel openings which serve either as gateways for collecting foraging material (foraging ports) or for the elimination of frass and/or mineral soil (Coaton, 1958; Moore & Picker, 1991; Grube, 2000; Uys, 2002). The foraging ports at Baba are similar to those of *H. mossambicus*, with star-shaped accumulations of grass culms around the foraging holes (Fig. S1a). These foraging ports are found in large numbers in the gradual transition between the vegetation-free bare patch and the fully developed matrix grassland (labelled TR in Fig. 5) and in the matrix vegetation—with slowly decreasing density away from the



Fig. 3. Baba fairy circles are larger than the FCs which are found further south. During most of the weeks in a year, the bare patch is devoid of living plants. After strong summer rains, annual plants such as *Tetraena simplex* can germinate and may grow for several weeks. Later these plants die and finally get removed sequentially starting in the centre and finally at the margin. The shown FC has a width of 18.3 m between left and right margin and 52.0 m from the foreground to the distant limit. [Colour figure can be viewed at wileyonlinelibrary.com].

FC. The termites are active during the early morning and later afternoon and even at midday when clouds or fog reduce the sunlight. Many dozens or even hundreds of small 1 dm high soil dumps (Fig. S1b) occur mainly near the centre of the bare patch, especially after the growing season of grass. The eliminated material consists partly of sand and partly—especially closer to the central nest—of frass.

- (5) *Lack of a perennial belt:* At the margin of the bare patch, there is no perennial belt of dense and taller long-lived grass plants, as is frequently found in the Namibian FCs.
- (6) *Sequence of circular belts:* Despite the lack of a prominent perennial belt, the Baba FCs can also be described as a sequence of circular belts that are characterised by different vegetation (Fig. 5a). In the centre of the BP, the powdery slightly elevated termite nest structure is almost always bare of vegetation. Only after very good summer rains, annuals like *Tetraena simplex* (L.) Beier & Thulin and *Trianthema triquetra* Rottler & Willd. grow for a couple of weeks (Fig. 3). At the margin of the bare patch, often a dark biological soil surface crust develops which more often allows growth of annuals (again mainly *T. triquetra* and *T. simplex*). Outside of the bare patch, there is a transition zone (TR) which (seen from the BP) starts with dead stumps of *Stipagrostis prodigiosa* (Welw.) De Winter, followed by live *S. prodigiosa* with basal leaves only. Further outside, there are live *S. prodigiosa* with single culms but no inflorescences. Finally, the outer transitional belt comprises live *S. prodigiosa* with single culms and low inflorescences form.

- (7) *Matrix vegetation:* The vegetation of the matrix is mostly dominated by living *Stipagrostis prodigiosa* plants with tall inflorescences. *S. prodigiosa* is the main foraging plant of the Baba termite. In many cases, *S. prodigiosa* is the only plant species. In other cases, a few herbs, a few individuals of the grasses *Stipagrostis uniplumis* (Licht.) De Winter var. *uniplumis* and *Schmidtia kalahariensis* Stent add less than 0.1% cover (see below for species). Only in one location near Rio Giraul, *S. giessii* forms the dominant grass, in the other locations, *S. giessii* was not present. In the coastal zone, *Tetraena simplex* and—less often—*T. triquetra* occur within the bare patch. Very frequently, i.e., sometimes in 100% of all FCs, there are holes of half a meter depth dug by aardvark (*Orycteropus afer*) foraging on termites. Months later, these holes form shallow depressions that collect rainwater resulting in small vegetation islands either of *S. prodigiosa* or *T. simplex* (Fig. S2). No cases were observed where damage by aardvarks caused the complete destruction of the termite colony within fairy circles. Especially at the plateau near Baba, *Euphorbia neochamaeclada* Bruyns is found in the matrix vegetation further away from the bare patches. After good summer rains, *Hirpicium gazanioides* Roessler, *Limeum viscosum* Fenzl, *Tephrosia dregeana* E-May., *Tribulus zeyheri* Sond., *Tripteris microcarpa* Harv. and several monocot geophytes are found. At the margin of the sandy landscapes where most Baba FCs occur, *Tetraena stapfii* (Schinz) with *Dactyloctenium aegyptium* (L.) Willd. and *Sesuvium crithmoides* Welw. sometimes form the neighbouring vegetation unit.

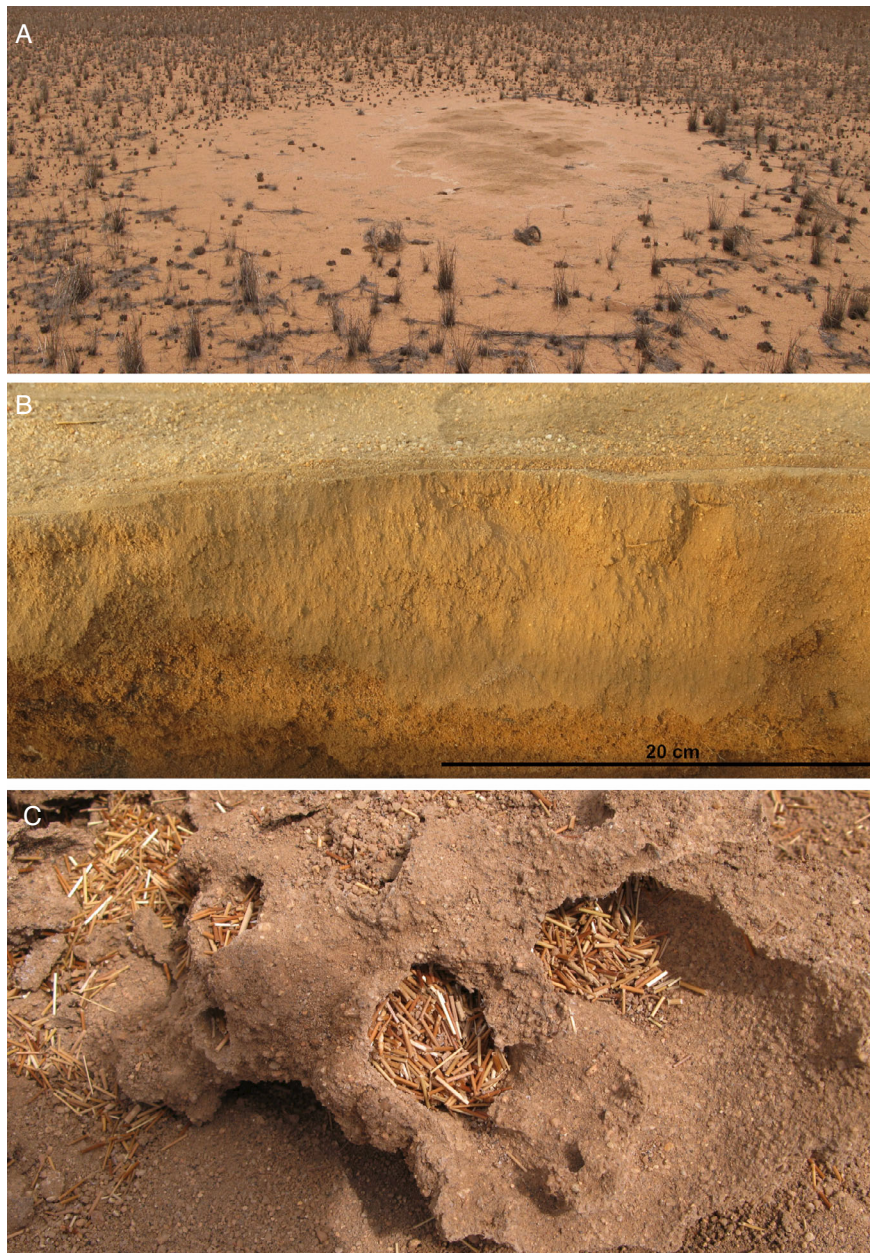


Fig. 4. Details of the fairy circles near Baba and their nest structure. (a) All Baba FC show shallow elevations of very fine powdery and saline soil material in the centre. These elevations are formed by termites. Underneath this powdery material tunnels and chambers are found which partly store cut grass culms. (b) Powdery saline topsoil in the bare patch centre, ejected by the termite colony. (c) Cemented chambers with stored grass culms, found underneath the powdery topsoil layer. [Colour figure can be viewed at wileyonlinelibrary.com].

Environmental features

(1) *Soil texture of landscape:* As with the Namib FCs further south, the Baba FCs occur in landscapes with homogeneous sandy topsoil. Large numbers of Baba FCs are found in level or slightly sloping plains which possess a deep, fine-grained soil without gravel, stones, blocks, or rocks. The median topsoil texture fractions in the matrix show 39.5% medium sand (0.2–0.63 mm grain size), 22.5%

coarse sand (0.63–2 mm grain size) and 14.5% fine sand (0.063–0.2 mm grain size) (Table 1, Fig. 5c).

(2) *Soil moisture:* Soil moisture was assessed using gravimetric measurements of soil samples collected along horizontal transects and down vertical profiles within the bare patch and the matrix. Horizontal soil moisture distribution is similar to the Namib FCs further south (Juergens, 2013): viz. underneath the bare patch, soil moisture is always higher (mostly >1% VWC), irrespective of the season

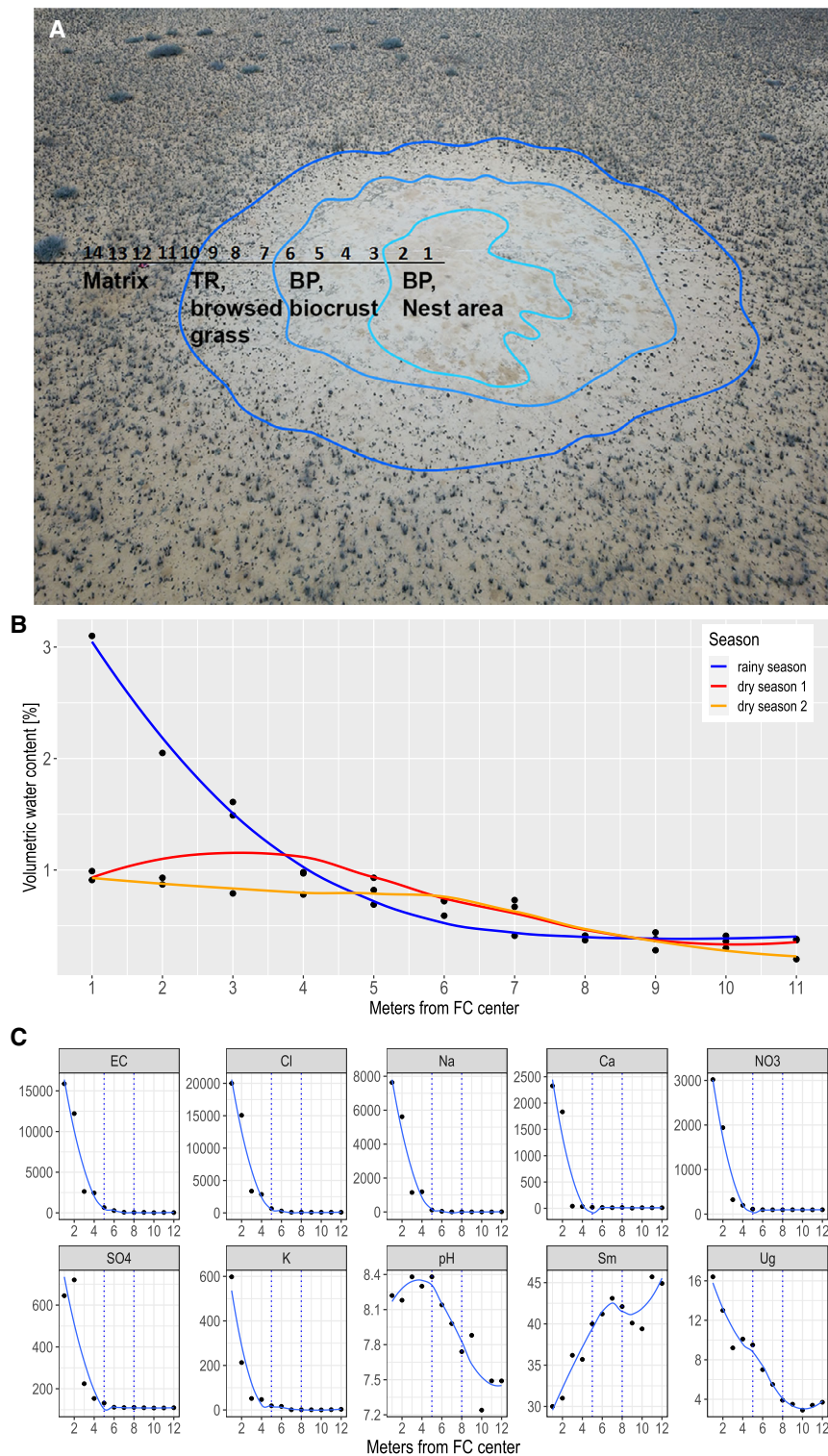


Fig. 5. Description of the Baba FC morphology and the corresponding soil analyses. (a) Drone picture of FC 32988 at Baba taken during the dry season on 2nd October 2018. Note the zonation showing the bare patch (BP) with the actual nest area and the consolidated marginal area with a biological soil crust and the continuous transition (TR) from bare patch to matrix (MT) vegetation. The figures indicate the radius in meters and correspond to the horizontal soil transects (b) and (c). (b) Soil moisture transects in Baba FC 32988 at 10 cm soil depth during various seasons. Blue = late summer (2014 04 29), 2 month after last rain; Red and orange = dry season before first rain (two FCs at 2014 10 28). MT = matrix, BP = bare patch. Scale in meter. (c) Chemical and physical soil parameters in Baba FC 32988 at 10 cm depth. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 1. Comparisons of soil parameters of fairy circle bare patch and matrix soil samples by paired Wilcoxon signed-rank test

Parameter	Bare patch		Matrix		Effect size	V statistic	p Value	
	Median	MAD	Median	MAD				
pH	8.12	0.31	7.88	0.24	0.388	98	0.129	n.s.
EC	2974	4284.86	40.75	22.34	0.840	133	<0.001	***
Coarse sand	18.63	5.96	22.5	4.32	-0.620	20	0.011	*
Medium sand	32.86	6.43	39.52	7.48	-0.738	11	0.001	**
Fine sand	15.71	6.58	14.05	5.58	-0.039	65	0.899	n.s.
Coarse silt	10.52	2.62	6.41	2.61	0.710	123	0.002	**
Medium silt	11.51	5.86	6.36	1.61	0.788	129	<0.001	***
Fine silt	5.48	2.04	3.74	1.06	0.725	124	0.002	**
Coarse clay	0.84	0.54	0.46	0.27	0.632	117	0.009	**
Fluoride	0.00	0.00	0.05	0.07	-0.385	7	0.141	n.s.
Chloride	678.37	1002.54	5.77	7.83	0.865	135	<0.001	***
Bromide	0.25	0.37	0.00	0.00	0.668	45	0.009	**
Nitrate	60.11	89.12	1.14	1.69	0.770	102	0.002	**
Phosphate	0.71	1.05	1.32	1.56	-0.645	4	0.011	*
Sulphate	20.13	29.24	0.88	0.93	0.815	131	<0.001	***
Sodium	805.22	944.77	20.72	14.98	0.840	133	<0.001	***
Potassium	83.61	81.92	3.01	3.4	0.880	136	<0.001	***
Magnesium	24.65	29.98	11.55	3.36	0.582	113	0.018	*
Calcium	14.02	20.03	1.79	1.97	0.852	134	<0.001	***

Note: The number of samples is $n = 16$ for each parameter. Median and median absolute deviation (MAD) are reported for bare patch and matrix. Effect size was determined by correlation (r). Large effect sizes are marked in bold. V and p -value are the respective statistics. n.s. = not significant; effect sizes: 0.10 to <0.40 = small; 0.40 to <0.80 = medium; ≥ 0.80 = large effect.

*** $p < 0.001$.

** $p < 0.01$.

* $p < 0.05$.

(Fig. 5b), than in the matrix soil (the latter with VWC decreasing to ca. 0% during the dry season).

- (3) *Soil physics and chemistry*: The properties of the powdery topsoil above the termite nest in the centre of the Baba FC have already been described above (see the section on “termite nest”, Table 1). All measured chemical soil parameters continuously decrease from the centre of the bare patch to the matrix (Fig. 5a, c). The same holds for the soil moisture (Fig. 5b) and all measured texture classes other than coarse- and medium sand which gradually increased from the bare patch centre towards the matrix (Fig. 5c). The bulk density is very low with $109.5 \text{ g}/100 \text{ cm}^3$ in the powdery material, compared to $145.5 \text{ g}/100 \text{ cm}^3$ in the cemented nest material further below and the bare patch soil at the outer half with $140.5 \text{ g}/100 \text{ cm}^3$. The matrix soil is packed much denser at $171.5 \text{ g}/100 \text{ cm}^3$.

Regularity of local spatial patterns

One conspicuous feature for which FCs are well-known is their regular spatial pattern in certain landscapes (Getzin *et al.*, 2015a,b; Juergens *et al.*, 2015). This spatial regularity, which is well developed in Namib FCs in landscapes with homogeneous topography and soils, is less pronounced in the Baba FCs (see Figs S2, S4, S5 and S6, Table S1). Due to the topography of all the Baba FC localities, there are only small areas where the land surface is homogeneous, without dry river beds or plateau escarpments. Therefore, in a first approximation, we

calculated density patterns using four $500 \times 500 \text{ m}$ plots (25 ha). The most striking difference between the Baba FCs and other studies on FC spatial pattern is the low density of the Baba FCs. While the overall number of observed Baba FCs in our study ranged from 141 to 214 per 25 ha (Table S1), Getzin *et al.* (2019) found very dense clusters of fairy circles with ca. 1800 FCs on 25 ha in Australia. Juergens and co-authors (2015) measured 1085 FCs in an area of 25 ha in the Giribes plains, Namibia. These two studies also found “strong” pair correlation functions with the model exceeding the simulated confidence bands. In our four plots (Figs S3, S4), the empirical pair correlation functions were much weaker, staying mainly within the confidence bands. This is probably caused by the low density of measured FCs; we kept the size of 25 ha to be comparable to the other studies. However, an extended dataset with more than 400 FCs (Figs S5 and S6, Table S1) yielded the same weak pattern. Hence another explanation could be the heterogenous environment, dampening the effect. The landscape is topographically considerably more heterogenous than the Giribes plains. This heterogeneity also led to varying shapes and areas of the analysis window which had to be accepted for the extended analysis. Still, the overall pattern is similar to that seen elsewhere (Getzin *et al.*, 2019; Juergens *et al.* 2015), i.e., regular spatial pattern with dominance of hexagonal Voronoi cells. Owing to the larger diameters of the circles, the nearest neighbour distances of the Baba FCs are twice as large as for the Namibian FCs. The minimum distance between FCs is around 10 m (except in BC2, Fig. S4b),

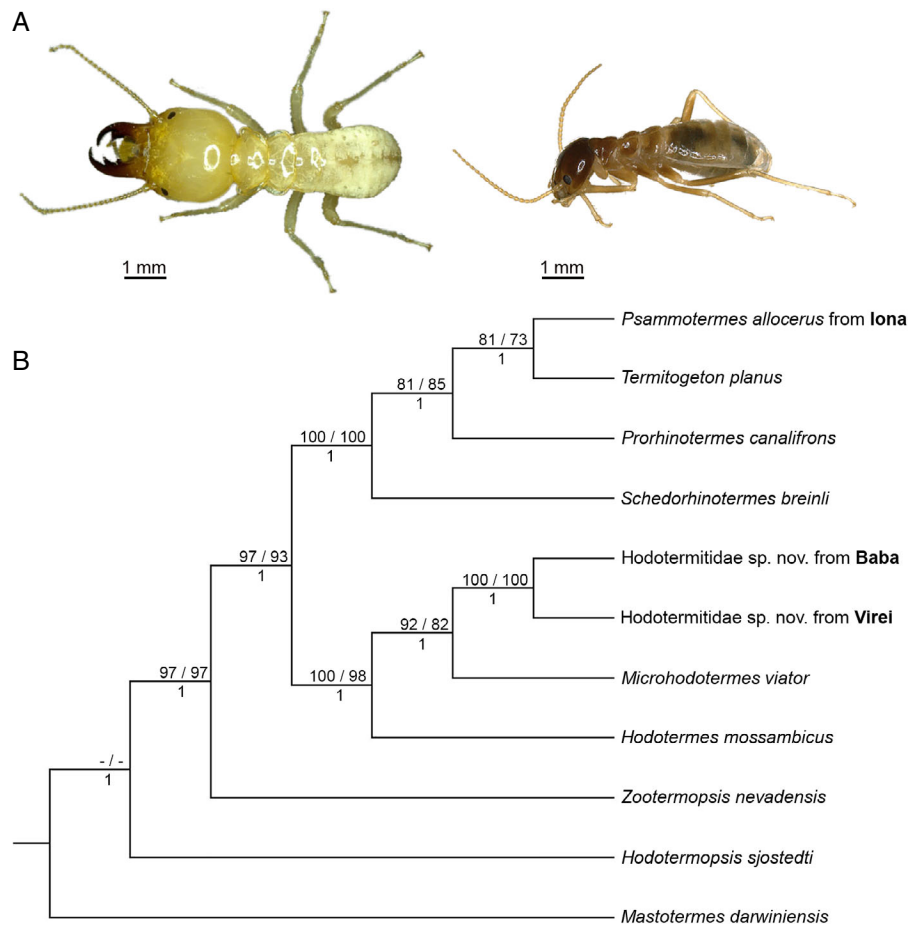


Fig. 6. Overview of the termites collected from FCs at Baba and their phylogenetic position in comparison to *Psammotermes allocerus*. (a) Soldier (left) and a worker (right) of the undescribed termite species *Hodotermitidae* sp. nov. 'Baba' found in the Baba FCs (Baba, Angola). They are genetically and morphologically part of the Hodotermitidae. (b) Phylogeny derived from the combined data set from the mitochondrial marker COI and COII. The posterior probability from the Bayesian inference is shown below the branches computed with a consistency index from 0.696 and a retention index of 0.500. The bootstrap support from the maximum likelihood is shown to the left, the maximum parsimony to the right above the branches. The '-' symbol indicates that a value under 50% was computed for this branch. [Colour figure can be viewed at wileyonlinelibrary.com].

the average nearest neighbour is found between 25 and 30 m (Table S1) and the density is between 6 and 8.5 FCs per ha.

It should be considered that the much larger spatial dimension of the single Voronoi cells of each FC must include more environmental heterogeneity. In consideration of this, and the lesser degree of landscape topographical homogeneity, the Baba FCs cannot produce the high regularity of the Namib FCs which are associated with *Psammotermes*. These environmental circumstances support the interpretation that the spatial pattern is sufficiently regular to be caused by competition among the neighbouring colonies.

Termites

The termites found in the Baba FCs differ from the termites found in the fairy circles south of 16.23°S. While even in Angola, south of 16.23°S, in all FC populations in almost each single FC, soldiers, workers, nests, sheetings, soil dumps, and

tunnels with a characteristic tapetum of *Psammotermes* Desneux (family Rhinotermitidae) are found, the FCs north of 16.23°S are inhabited by an unknown and apparently undescribed species of termite (Fig. 6a) previously identified as a species of the Hodotermitidae (Vivienne Uys pers. comm.). Therefore, we decided to clarify the taxonomic position of the termites based on molecular genetics and gross morphology.

Phylogenetic position of the Baba termite

The topology of all phylogenetic trees for samples of 11 termite taxa showed the same pattern (Fig. 6b) and similar statistics. The COI data had a total length of 806 characters, 62.3% (502 nucleotides (nt)) were constant, 37.7% (304 nt) were uninformative and 29.9% (241 nt) were parsimony-informative characters. The alignment of the COII marker was slightly shorter with 657 characters. The number of uninformative characters with 52.5% (345 nt) and of parsimony-informative

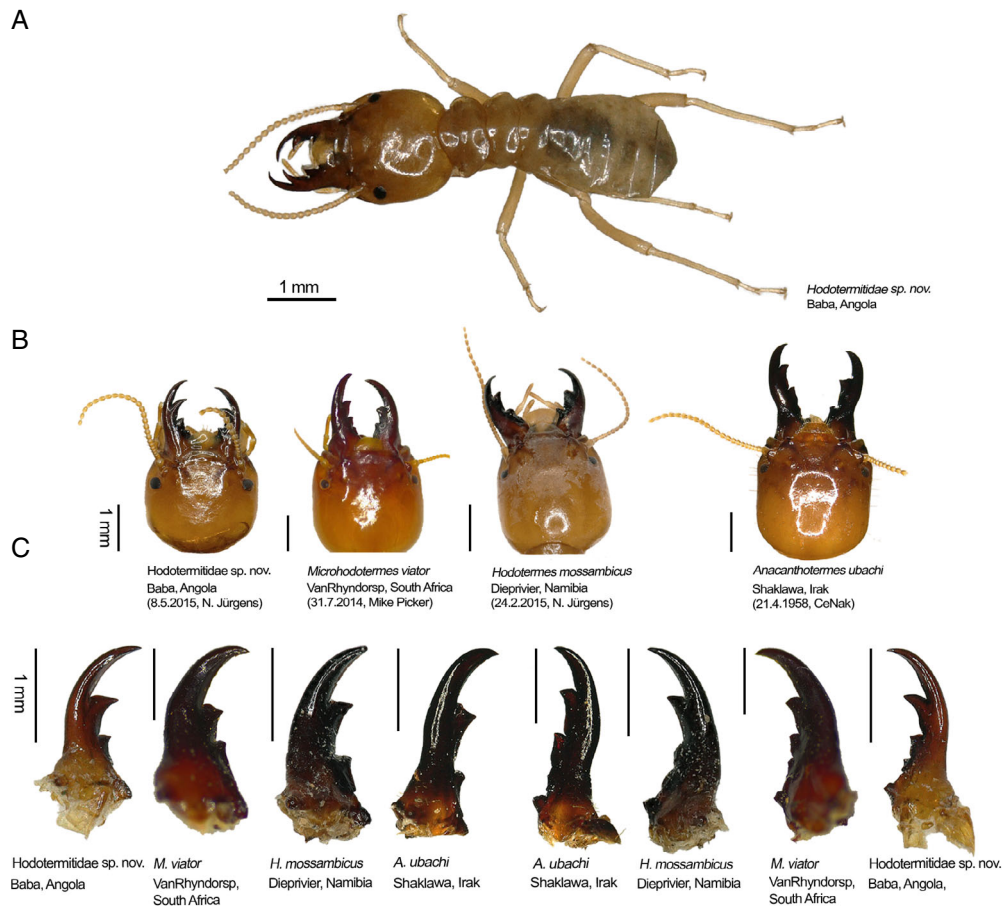


Fig. 7. Comparison of mandibles and heads of soldiers of *Hodotermitidae sp. nov.* ‘Baba’, *Microhodotermes viator* (VanRhynsdorp, South Africa), *Hodotermes mossambicus* (Dieprivier, Namibia) and *Anacanthotermes ubachi* (Shaklawa, Irak, loan from CeNak, University of Hamburg). (a) A termite soldier of Baba FCs. (b) The heads are compared (dorsal view) and in (c) the mandibles (ventral view). The first four show the right mandibles and the following four the left mandibles. [Colour figure can be viewed at wileyonlinelibrary.com].

characters (37.7%, 248 nt) were higher. For this marker, 46.3% (304 nt) were constant. The combined dataset with a total length of 1463 characters consisted of 57.3% constant characters (838 nt), 42.7% uninformative (625 nt) and 31.9% informative characters (467 nt).

The family Hodotermitidae could be delimited from the outgroup and the other termite families Archotermopsidae and Rhinotermitidae with very good support (posterior probability (PP) = 1, bootstrap support (BS) = 100% in the ML and 98% in the MP) in all combined phylogenetic analyses (Fig. 6b). The unknown termites from Virei and Baba are sister taxa and form a genetically well-separated group (PP = 1, BS of ML and MP = 100%). The two taxa are more closely related to *M. viator* than to *H. mossambicus*. The respective GenBank sequence of *M. viator* originates from a collection by Cameron made near Worcester, South Africa (Table S2).

The position of *P. allocerus* is well supported within the Rhinotermitidae and appears as sister to *Prorhinotermes canalifrons* without maximum parsimony (BS = 73%) but with moderate maximum likelihood (BS = 81%) support and a very good posterior probability value of 1.

The genetic differentiation is also supported by comparisons of morphological characters of the outer head and mandible of the soldiers of the *Hodotermitidae sp. nov.* ‘Baba’, *M. viator*, *H. mossambicus* and *Anacanthotermes ubachi* (Fig. 7a–c). In the dorsal view of the individual heads, a difference in shape is discernible. The head of both *Hodotermitidae sp. nov.* ‘Baba’, is rounder than the heads of *H. mossambicus* and *A. ubachi*. The head of *A. ubachi* alone is somewhat hairy and was previously described (Harris, 1967) as rectangular with slightly concave sides. The eyes of the *Hodotermitidae sp. nov.* ‘Baba’ are larger than those of the other three species within the Hodotermitidae (Fig. 7b), dorsal view).

More obvious differences can be seen in the morphology of the mandibles: The right and left mandibles are presented in a contrasting juxtaposition (Fig. 7c, ventral view). The mandibles of the new species from Baba are of a much lighter colour, compared to the darker mandibles of *H. mossambicus*, *A. ubachi* and *M. viator*.

Also, the shape of the individual teeth differs. The right mandibular plate and the apical tooth of the *Hodotermitidae sp. nov.* ‘Baba’ are much slimmer than those of *M. viator* and

H. mossambicus. In addition, the molar plate of *A. ubachi* is slimmer than and almost as wide as the entire mandible. The first marginal tooth (m_1) of *M. viator* and *A. ubachi* shows a wave towards the apical tooth. The m_1 in Hodotermitidae sp. nov. “Baba” is longer stretched towards the inside and has only a small elevation to the second marginal tooth. The m_1 of *H. mossambicus* is smooth without any additional shape. Differences are also visible in the shape of the left mandible of these four species.

The left mandible of the Hodotermitidae sp. nov. “Baba” is much narrower overall compared to that of *H. mossambicus* and *M. viator*. The molar plate is similarly narrow in *A. ubachi*, as is the whole left mandible. The apical tooth of the Hodotermitidae sp. nov. “Baba” is distinctly longer and narrower than the apical tooth of the other species. Furthermore, the first marginal tooth of *A. ubachi*, *H. mossambicus* and *M. viator* to the inside is shorter than that of the unknown species. The m_1 is also curved in *A. ubachi*, *M. viator*, and Hodotermitidae sp. nov. “Baba”. Additionally, the m_1 of these species has a wavy shape to the second marginal tooth. The curved and wavy shape is not recognizable in *H. mossambicus*.

Finally, it appears that the left mandible of *M. viator* and of Hodotermitidae sp. nov. “Baba” show similarities in the shape of single individual teeth, but there are clearer differences in the morphology of the right mandible.

The family Hodotermitidae includes the genera *Hodotermites*, *Microhodotermites*, and *Anacanthotermites*. After comparison of *Anacanthotermites ahngerianus*, *A. macrocephalus*, *A. ochraceus*, *A. ubachi*, *Hodotermites mossambicus*, *Microhodotermites viator*, and available literature descriptions of *Hodotermites erithreensis* (Sjöstedt, 1912), *Microhodotermites wasmanni* (Sjöstedt, 1900), and *M. maroccanus* (Sjöstedt, 1925), we are able to say that the termite species from Baba is not conspecific with any of these. Therefore, we regard the Baba termite as an undescribed species within the family Hodotermitidae. Furthermore, the available data on molecular phylogeny, morphology, nest architecture, and foraging behaviour suggest that the new species shares more characteristics with the genus *Microhodotermites* than with the other two genera of the family. However, we keep the option open that the taxon could merit the status of a new genus if additional data should support such a view. Therefore, we presently use the term Hodotermitidae sp. nov. “Baba” for this taxon.

Baba FCs encompass properties found in the ecosystems engineered by *Psammotermes allocerus* and by *Microhodotermites viator*

1. *Baba FCs share properties with Psammotermes FCs*: Until now, Namib fairy circles have been regarded as uniform, in principle, with some characters such as diameter, changing slowly across space as a continuous gradient (Cramer & Barger, 2013; Jürgens, 2013). Therefore, Baba FCs have so far been regarded as a subset of Namib fairy circles. Both share many similarities, including (a) the roughly circular bare patch, (b) the preference for sandy soils, (c) the functional property to store rainwater even during

prolonged periods of drought, (d) the association with a termite colony, (e) the biogeographical continuation of the Namib fairy circle belt, without a major disruption in terms of space or environmental conditions, (f) the formation of a regular spatial dispersion pattern.

2. *Baba FCs differ from other FCs*: However, several properties clearly distinguish the Baba FCs from those FCs occurring further south, including, (a) the significantly larger size of the bare patch, (b) the lack of a perennial belt, (c) the formation of the Baba FCs within a matrix of the endemic grass species *S. prodigiosa* (compared to the matrix grasses *S. giessii*, *S. uniplumis*, *S. ciliata*, *S. obtusa*, *S. geminifolia* in the case of *Psammotermes* FCs), (d) the extremely high soil salinity in the topsoil of the bare patch centre, (e) the location of a single epigeal termite nest of several meters diameter near the surface in the central region of the bare patch. This nest differs markedly from the nest system of *Psammotermes* in the FCs occurring further south, which is composed of numerous roundish or cylindrical nests in a dimension of several cm to a few dm, interconnected by narrow tunnels (Jürgens, 2013). Additionally, (f) the soil dumps show no similarity to the much smaller soil dumps formed by *Psammotermes* (Jürgens, 2013) and (g) isopods are present in the termite nests in the Baba FCs and nests of *M. viator* (Coaton, 1958) but not in *Psammotermes* FCs.
3. *Baba FCs share properties with M. viator engineered ecosystems*: Most important from an evolutionary point of view are a number of similarities shared by the Baba FCs with *M. viator* colonies in the dry parts of the Northern Cape of South Africa, including (a) the epigeal nest in the centre of the bare patch and the slight elevation which is similar to one of the surface manifestations of *M. viator* (McAuliffe *et al.*, 2019b), (b) the accumulation of soluble salts in the topsoils of the bare patch centre as shown by McAuliffe *et al.* (2014), McAuliffe *et al.* (2019a,b), (c) the colour change from blackish to whitish in the weathering layer of frass found on top of nests of the Hodotermitidae sp. nov. “Baba” in Angola and of *M. viator* in the Succulent Karoo of South Africa, (d) the presence of grass storage chambers in the nest, some of which are filled with blackish frass as described for *M. viator* in the Karoo of South Africa (Coaton, 1958; Moore & Picker, 1991), (e) the morphology of foraging holes and excavation ports, (f) the frequent destruction caused by aardvark, were also described for *M. viator* (Moore & Picker, 1991; McAuliffe *et al.*, 2019b) where 53% of all mounds were excavated, (g) the lack of a perennial belt and (h) regularity—though not extremely regular—of the spatial pattern (McAuliffe *et al.*, 2019a).
4. *Baba FCs differ from M. viator engineered ecosystems*: Lastly, there are also properties which distinguish the Baba structures from *M. viator* structures. First, Baba FCs prefer landscapes with sandy soils as compared to the more silty-loamy soils preferred by *M. viator*, which marks an essential functional difference. Sandy soils allow for more rapid penetration and percolation of short intensive rain from thunderstorms, typical for the convective tropical summer rainfall system. In contrast, the more loamy soils at *M. viator* colonies allow slow penetration of rainwater in the

winter rainfall system of the Karoo biomes with its typical cyclonic steady rain or drizzle, sometimes falling over more than a day. Second, the slight central elevation of Baba FCs is an accumulation of frass excreted by the termites and therefore not homologous to *M. viator* earth mounds (heuweltjies) which are generated by aeolian sediment accretion.

In summary, the Baba structures share properties of both, *Psammotermes* FCs and nest systems of *M. viator* (Coaton, 1958, 1962; McAuliffe *et al.*, 2019a,b). In many respects, the Baba system exactly mirrors very distinctive properties of the colonies of *M. viator* like the composition of those anions and cations which are similarly found in the frass deposited above the nests at Baba and as well in the Succulent Karoo, despite the 1.200 km geographical distance between their distribution ranges. In many other respects, the Baba structures exactly match the properties of the Namib FCs, in that they prefer sandy soils, store rainwater in the soil of their bare patch. They even geographically perpetuate the narrow band close to the 100 mm isohyet inhabited by Namib FCs further south into Angola until these arid conditions reach their northernmost limit and taper out at the Atlantic coast.

Some of the main differences that distinguish the Baba FCs from the *Psammotermes* FCs can be explained by the different nesting and foraging adaptations of the termites involved.

The lack of the perennial belt is a consequence of the Baba termite's foraging which—after a good growth period—progresses from the bare patch outwards, as indicated by the highest density, at any observed time, of foraging holes adjacent to the bare patch in the transition zone (TR) (Fig. 5a). Foraging holes decrease in density further away from the BP, however, they do constantly occur also in the outer matrix. These observations may indicate an oscillating foraging strategy which after good rains expands the foraging area to larger distances, thereby causing competition with neighbouring colonies, and which focusses on the area closer to the nest during dry periods. These observations are also in line with the foraging behaviour of other Hodotermitidae which also harvest areas in large distance to the central nest site. For example, Coaton (1958, 1962) recorded *Microhodotermes viator* colonies in the Eastern Karoo, foraging to a radius of 45 m around its hive. Like other Hodotermitidae, also the Baba termites forage also during the day, especially when the coastal fog provides shade and cool temperatures.

In summary, we interpret the spatial pattern and regular distance as being a consequence of competition between neighbouring termite colonies, following a more general concept (Tarnita *et al.*, 2017). A time comparison of FCs at Baba, Pipa and Chapeu Armado in satellite images from 2004 until 2019 (offered by Google Earth) reveals no turnover of these FCs but only an expansion and reduction of their transition zone. The above observations would match the notion of an oscillating gradually increasing and decreasing bare disc and termite colony, depending on the available biomass of the given year. This would also be in line with the observation that all the chemical and physical soil diameters show a gradual change from the centre into the matrix area (Fig. 5). There is no abrupt discontinuity.

Discussion

In this study, we have shown that in different geographical regions of the Namib Desert members of two different termite families generate structures which hitherto have been widely accepted as homogeneous Namib fairy circles. We also presented evidence that the two types of FCs are two distinctive entities characterised by different morphology, processes and functions.

The similarities and differences can be explained from the ecosystem engineering of the termites involved. The observed similarities of the structures, which are either engineered by Hodotermitidae sp. nov. “Baba” termites in the case of the Baba FCs or by *Psammotermes* termites in the case of the more southern FCs, are interpreted as an interesting example for parapatric convergent evolution of nest systems of desert termites. In addition, the striking similarities between many properties of the Baba structures and the more southern *M. viator* structures (heuweltjies) also provide additional support for a termite origin of the ‘heuweltjies’ in the Karoo and the Cape.

While the phylogenetic position of the Baba termites (in the family Hodotermitidae) and the more southern Namib FC termite (in the genus *Psammotermes* in the family Rhinotermitidae) define a strict discontinuity, the structures and properties of the two ecosystems engineered by these two termite species show a number of similarities.

In summary, the newly described structures are neither classic FCs nor *M. viator* heuweltjies but a structure “sui generis”. Unfortunately, there is no uniform terminology to describe structures and ecosystem functions of social insects.

Therefore, for the time being, we propose to refine the terminology of fairy circles and to use the name of the causative social insect as part of the name of the engineered ecosystem, i.e., to split the Namib FCs into the more southern “*Psammotermes* fairy circles” and the Angolan “Hodotermitidae Baba giant circles”.

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The authors declare no conflict of interests.

Author contributions

NJ designed research, NJ, FG, IO, JRH, performed field research, NJ, FG, JO, AG, JRH, IO, and MP analysed data, NJ, FG, JO wrote draft paper, all contributed to improving the analyses, the interpretations and the manuscript.

Data availability statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supplementary text: Material and Methods

Fig. S1: Foraging holes and soil dumps of *Hodotermitidae* sp. nov. “at Baba”.

Fig. S2: Baba fairy circle with a central grass island of *Stipagrostis prodigiosa*

Fig. S3: Location of study sites for PCF analyses

Fig. S4: Pair correlation functions

Fig. S5: Sampling areas for second pattern analysis

Fig. S6: Pair correlation functions for second pattern analysis

Table S1: Summary statistics of Baba circle point patterns.

Table S2: Species sample accession numbers received from GenBank.

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