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**Biodiversity & Ecology 7**

# Fairy Circles of the Namib Desert

Ecosystem engineering by subterranean social insects

Southern Namib. During the progress of evolution this is the first taxon in the phylogenetic tree of the sand termites that is adapted to survive in a world without woody plants but only grass. Two populations of this genetic group occur somewhat further east in fairy circles at Gariganus and in vegetation without fairy circles near Keetmanshoop (Fig. 4.12).

At the next layer, the phylogenetic tree shows a large group that inhabits the region further north and further east in Namibia and parts of South Africa. The first subclade (0.95 pp) includes three genetic groups: These three groups inhabit (a) the East Gariiep region in the Orange Valley and south-eastern Namibia (dark green), (b) the south eastern Kalahari Dunes (light green) and (c) the southern Namaland (yellow). Termites of these three groups were found likewise in fairy circles and in landscapes without fairy circles, feeding either on grasses or also on dead wood.

The second subclade (0.96 pp) comprises the “Western Kalahari Basin” (ochre) and “Northern Namib” (red) group. The “Western Kalahari Basin” taxon has a very large area of distribution which includes populations from Katima Mulilo (KM) in the far north-east to Swartkop (SK) in the south-east of Namibia. Termites of the uppermost clade “Northern Namib” are found from Gobabeb (GB) in the south to the Iona National Park (IO) in Angola.

This phylogenetic differentiation is further supported by additional molecular statistical analyses regarding the high mean p-distances between the groups, the high number of haplotypes between the groups, and the high number of unique haplotypes within the median joining network (data not shown, and Gunter et al. 2022).

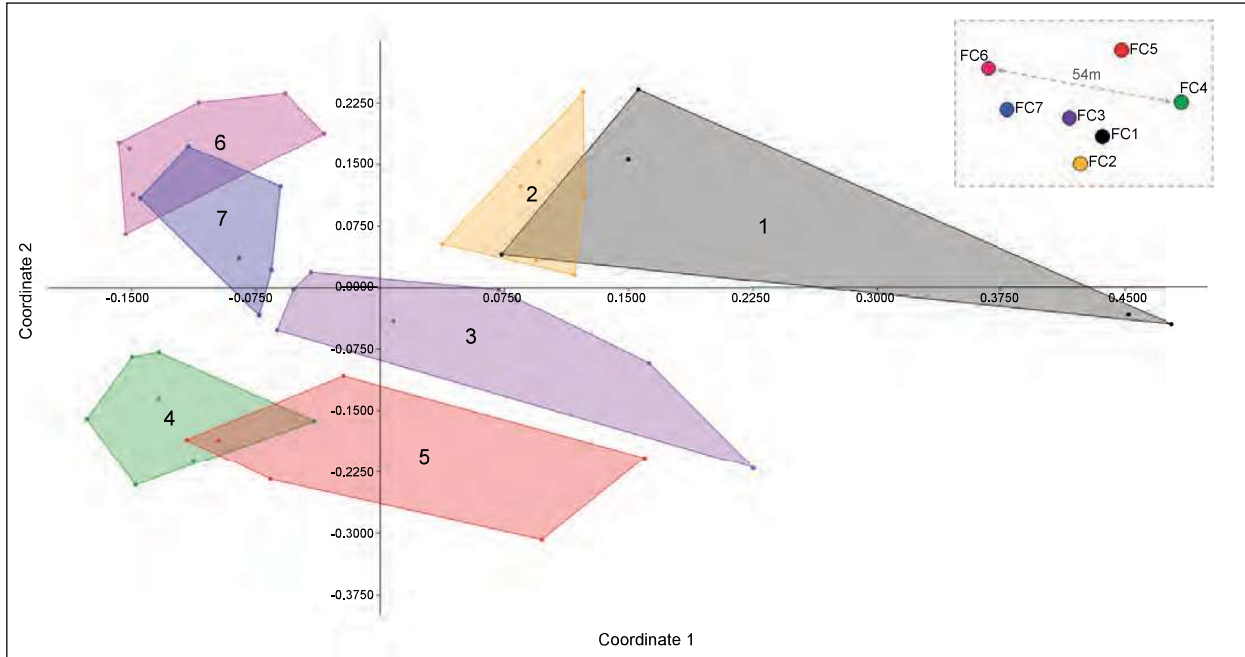
These molecular results and observations from the field show that *Psammotermes allocerus* cannot be regarded as one single species but as an aggregate of several closely related species. According to Gunter et al. (2022), the species name *P. allocerus* should be limited to populations of the genetic group “Succulent Karoo” due to the type collected at Lüderitz. The other genetic groups should receive new species names and are here presented with preliminary names using the terminology of the genetic groups e.g., *Psammotermes* spec. “Northern Namib”.

## Reproduction of sand termites and local genetic patterns

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According to Coaton & Sheasby (1973), winged queens and kings can be observed from March to December. The reproductive animals then wait in the tunnel system of the nest (Fig. 4.14). This unusually long waiting period and alate season, compared with other termites, was interpreted by Coaton & Sheasby (1973) as an adaptation to the unpredictable rainfall in the arid climate. Typically, swarming occurs the day after the first heavy rainfall in a given season. We noted that most swarming occurs in the morning after a good initial rain event. Depending on weather conditions and especially the wind speed, several dozen to a few hundred individuals were observed in the air at a site with a cluster of fairy circles. The observations of travel speed and landing distance made so far suggest a spatial displacement of only a few hundred metres to a few kilometres for the majority of alates. However, rare long-distance even trans-oceanic dispersal events are possible (Hellemans et al. 2022). After a short time (from less than one to a few hours), the winged termites (alates) land and can be observed shedding their wings at predetermined breaking points (Fig. 5.3). Subsequently, we observe mostly pairs in which a male individual follows a female individual (Fig. 5.4) and sexual mating occurs. Subsequently, a queen and king (Fig. 4.22) produce eggs in their royal chamber during a period of unknown length; the eggs are then nursed into offspring and develop into different castes, e.g. workers and soldiers.

The sand termite species belongs to the family *Rhinotermitidae*, which is particularly characterised by the developmental pathway from an egg to the juvenile and worker or soldier up to reproductives (king and queen), and which differs greatly in its expression between several species (Roisin & Lenz 1999). Regarding the genus *Psammotermes*, only the developmental pathway of *P. hybostoma* from Egypt has been described in more detail (Bourguignon et al. 2012). To date, no one has accurately studied the morphological life cycle of the sand termite from the fairy circles. In addition to morphological studies of different castes, the investigation of gene flow and genetic similarity or dissimilarity of neighbouring colonies can also provide insights into



**Figure 4.13:** Result of the PCoA of termites from seven neighbouring fairy circles in Dieprivier, Namibia. The inserted graph in the above right corner shows the spatial pattern of the seven sampled fairy circles and a scale of 54 m.

the reproduction biology and founding of new colonies. This was investigated by Brandl et al. (2005), who studied the gene flow between distant populations of *Macrotermes michaelseni*. The analysis of the genetic diversity of neighbouring termite colonies from fairy circles was part of a master thesis (Bohn 2014) in our research group and the PhD thesis of Felicitas Gunter. For this purpose, termites from seven neighbouring fairy circles, so-called clusters, were studied using the amplified fragment length polymorphism method (AFLP) from five different fairy circle areas (Iona, Marienfluss Valley, Giribesvlakte, Dieprivier and Springklippvlakte). The AFLP method is a generally accepted method to analyse genetic diversity and genetic distances of individuals from different populations. The main questions of interest were whether the termite colonies of spatially neighbouring fairy circles arise by the migration of a new queen directly from the neighbourhood (hypothesis 1) or whether new fairy circles arise when queens from far away fly in and land (hypothesis 2). In the latter case, much greater genetic dissimilarity would be expected. Preliminary results (Fig. 4.13) reveal a high genetic dissimilarity among termites of neighbouring fairy circles. The Principal Coordinate Analysis (PCoA) shows high genetic distances between the fairy circles at Dieprivier. Although some fairy circles slightly overlap, statistical results show significant differences

between them. This result supports the second hypothesis that new fairy circles arise from the entry of alates from further away.

**Recommended citation:**

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**Figure 4.14:** Alates (winged future *Psammotermes* queens and kings) in their waiting position within the tunnel system of a sand termite nest (Giribesvlakte Biodiversity Observatory, 19.03.2017).