

# Phylogeny of sand termites

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Carabidae (Sasakawa 2016), or wing venation geometry in insect taxa (e. g. Lorenz et al. 2017). The shape of soldier mandibles and head capsules were often used to identify species between several genera of different termite families (Weesner 1970; Eggleton 2010). So far, the mandible shape was not investigated with the GMM method. Our results show that the selected seven landmarks show a strong power of differentiation between these three groups. A quantitative assessment of morphological differences within *P. allocerus* seems reasonable, resulting in species-specific morphological traits (Hausberger et al. 2011), facilitating faster identification. In addition to the mandible shape, several traits of the degree of pilosity of the head and dimensions of the head capsule, labrum and mandible (Tab. 4.3) allow differentiation. A similar intra-specific variation was documented for *Cubitermes* species (Roy et al. 2006).

We demonstrated the feasibility of using the CART method for our data set and conclude that traditional measurements and the shape of soldier mandibles can help discriminate and identify considerable differences within a species. Large soldiers of *P. allocerus* from these studied groups are not homogeneous in their morphological expression. The investigated differences are consistent with the subdivision into the three bioregions. In their genetic study of the species complex of *P. allocerus*, Gunter et al. (2022; Gunter et al. 2022 see the following Chapter 4.4.4) suggest allopatric speciation. The relationships between the morphological differences and different environmental factors would need to be further illuminated in the future. We are aware that characteristics can also vary within a species, as described for East African *Cubitermes* species (Roy et al. 2006; Williams 1966). Up to 10 different soldier instars which differ in head and pronotum width were described for *P. hybostoma* (Bourguignon et al. 2012). Our study should be regarded as a first attempt to illuminate hidden differences within the southern sand termite. In the future, the dataset should include additional developmental stages of soldiers. An extension of the study area to the other species within the *Psammotermes* species complex (Gunter et al. 2022; 2022 in the Chapter 4.4.4), to more humid areas within South Africa (Eastern Cape, Western Cape, St. Lucia) and more eastern and northern taxa, e.g., *P. hybostoma*, will hopefully allow formal taxonomic decisions.

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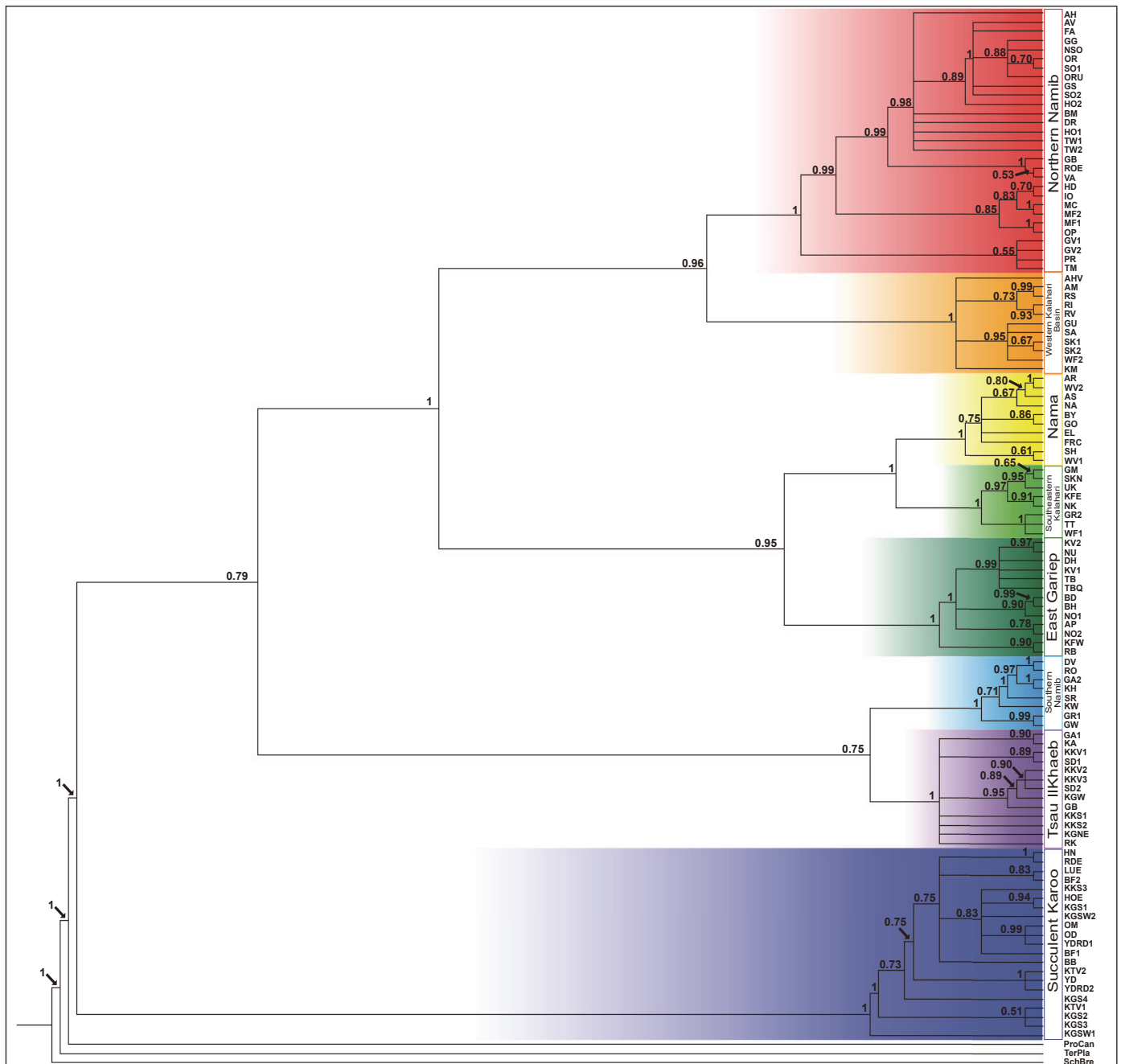
The sand termite *Psammotermes allocerus* is one of the ecologically most important termites in the arid ecosystems of the Namib Desert in terms of distribution (Coaton & Sheasby 1973) and adaptation to a wide spectrum of different hyperarid habitats (Zeidler 1997). Our current study of the sand termites and their causative role in the fairy circles revealed distinct differences in several features in various geographic areas. For example, termite nests in the Succulent Karoo have light-coloured tunnel walls, while in all other regions, the tunnel walls are lined by a blackish tapetum. Only in the Succulent Karoo are nests positioned in the topsoil not deeper than 50 cm (Gunter et al. 2022).

Gunter et al. (2022, this volume, Chapter 4.4.3) could show morphological differentiation within three groups of the sand termite based on large soldier characteristics only. (For a later full taxonomic revision additional instars of soldiers or other castes for the entire area of distribution will have to be included). Beside morphological based taxonomy, DNA barcoding became an important method to distinguish species (Hebert et al. 2003) or to reveal hidden species complexes in termites (Gunter et al. 2022; Austin et al. 2007; Roy et al. 2006). An integrative respectively iterative taxonomic approach was proposed by several authors (Bourguignon et al. 2013; Dayrat 2005; Will et al. 2005) to delineate taxa. In the past, only few molecular phylogenetic studies included sand termites (Inward et al. 2007b; Jürgens et al. 2020). Therefore, the evolution of the sand termites of the wider Namib Region was reconstructed by Felicitas Gunter using molecular genetic methods as part of her dissertation in the Department of Biology at the University of Hamburg. This study included 64 sand termite samples. Based on additional samples that were mainly collected within the Tsau I Khaeb National Park in September and October 2022, the here shown phylogeny comprises 113 sand termite collections.

The diversification of sand termites in time and space is shown in the phylogenetic tree (Fig. 4.11 and Fig. 2 in Gunter et al. 2022). Eight different groups are very well differentiated based on the support values of the clades. According to this tree, the most basal clade of the arid-adapted sand termites originated in the Succulent Karoo

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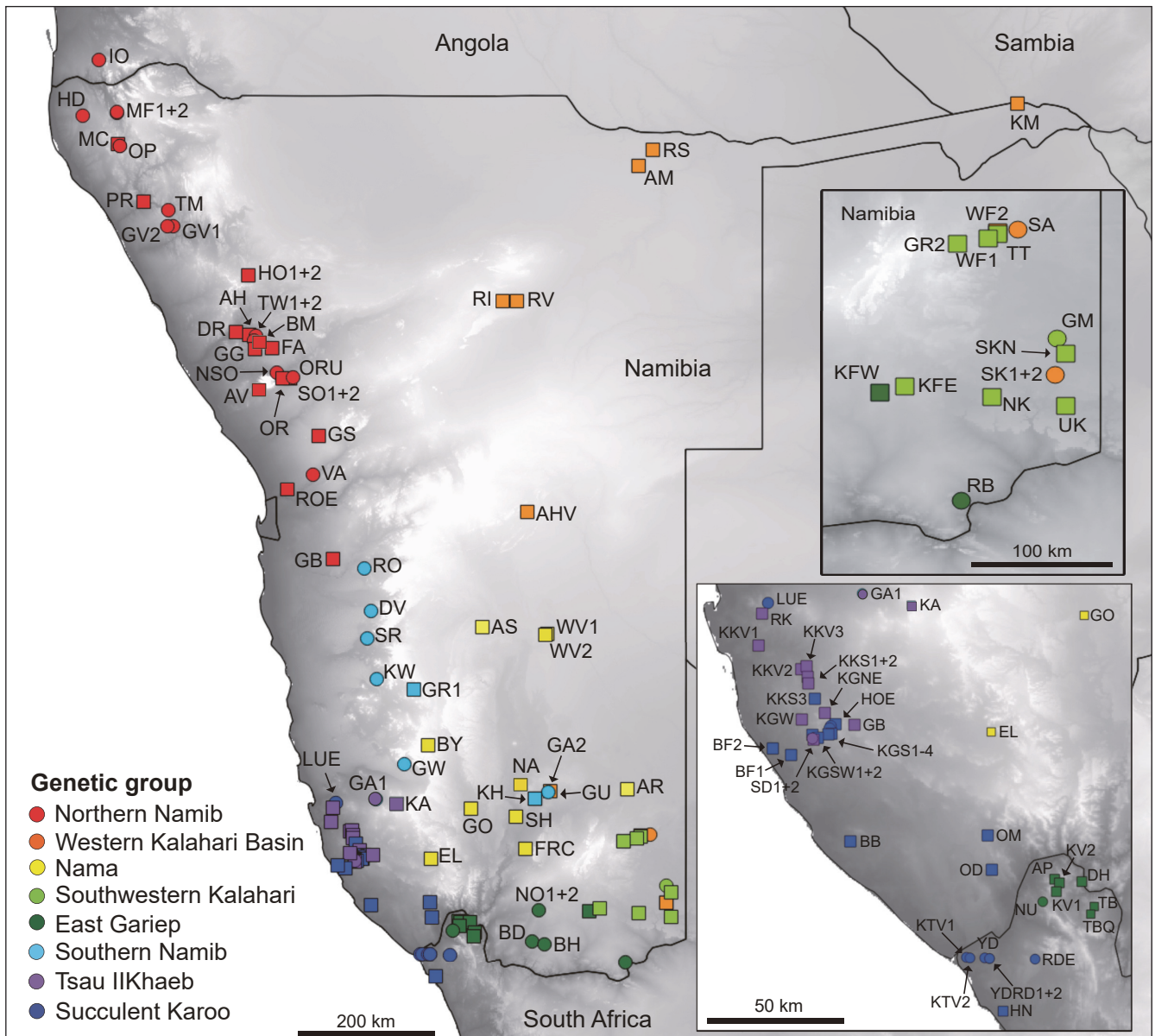
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**Figure 4.11:** Phylogenetic tree of *P. allocerus* samples from southwestern Africa (Data and graphics: F. Gunter). Abbreviations of study sites are shown in Figure 4.12.

biome of the Greater Cape Region, including Namaqualand and the coastal plain of the Richtersveld in South Africa and the southwestern parts of the Sperrgebiet in Namibia near Lüderitz (marked dark blue in Figures 4.11 and 4.12). Here, in the arid Succulent Karoo biome, *Psammotermes* forages on the woody vegetation formed by “living stones” (e.g., species of the genus *Brownanthus*) in the family Aizoaceae, but also on Asteraceae and a few grass species. Only in the more arid parts of its distribution area, i.e., in the coastal plain of the Richtersveld and the Sperrgebiet, does this genetic group of *Psammotermes* form fairy circles in the vegetation.

Further up in the tree, the phylogeny reveals two taxa “Tsau lKhaeb” (purple, Fig. 4.11) and “Southern Namib” (light blue). Both are sister to each other (0.75 posterior probability support (pp)) but very well separated (pp = 1). Both taxa occur in the summer rainfall region within Namibia (Fig. 4.12). Sand termites of the “Tsau lKhaeb” taxon feed on grasses and on wood of *Euphorbia gummifera*. Thereby, and by the geographical occurrence close to the winter rainfall zone, the “Tsau lKhaeb” taxon shows similarities to the “Succulent Karoo” taxon. Termites of the “Southern Namib” taxon colonize mainly the grasslands of the desert margin of the



**Figure 4.12:**

Geographic locations of taxonomic units shown in the phylogenetic tree (Fig. 4.11) according to F. Gunter et al. (2022) (data and graph: F. Gunter). Circles represent fairy circle samples; squares represent collections that were not acquired in a fairy circle.

**Northern Namib:** (AH) Aba Huab rivier, (AV) Averbas, (BM) Burnt Mountain, (DR) Die Riet, (FA) Farm 522, (GB) Gobabeb, (GG) Goantagab, (GV1) Giribesvlakte, (GV2) West of Giribesvlakte, (HD) Hartmann, (HO 1+2) Hoadia, (IO) Iona, (MC) Marbel Camp, (MF1+2) Marienfluss, (NSO) North of Brandberg, (OP) Onjuva Plain, (OR) Okambahe Reserve, (ORU) Okambahe Reserve North Uys, (PR) Purros, (ROE) Rössing Mountain, (SO1+2) Sorris Sorris, (TM) Tomakas, (TW1+2) Twyfelfontein, (VA) Valencia;

**Western Kalahari Basin:** (AHV) Alt-Hartebeestvlei, (AM) Alex Muranda, (GU) Gariganus, (KM) Katima Mulilo, (RI) Rimini, (RS) Rundu South, (RV) Ravenna, (SA) Samehaling, (SK1+2) Swartkop, (WF2) Warmfontein;

**Nama (Namaland):** (AR) Averbas, (AS) Auros, (BY) Barby, (EL) Elbra, (FRC) Fish river Canyon, (GO) Goageb, (NA) Namaland 4, (SH) Seeheim, (WV1+2) Witvley;

**Southeastern Kalahari:** (GM) Goedmoed, (GR2) Gurus, (KFE) Kalkfontein East, (NK) Neikop, (SKN) Swartkop North, (TT) Tranental, (UK) Ukamas, (WF1) Warmfontein;

**East Gariep:** (AP) Akadispass, (BD) Belda, (BH) Bruinheuwel, (DH) De Hoop, (KFW) Kalkfontein West, (KV1+2) Koeroegabvlakte, (NO1+2) Norachas, (NU) Numees, (RB) Rooiberg, (TB) Tatasberg, (TBQ) Tatasberg Quarzfeld;

**Southern Namib:** (DV) Dieprivier, (GA2) Gariganus, (GR1) Gorab, (GW) Gunsbewys, (KH) Keetmanshoop, (KW) Keerweder, (RO) Rostock, (SR) Sesriem;

**Tsau Iikhaeb:** (GA1) Garub, (GB) Gabusib North, (KA) Klein Aus, (KGNE) Klinghardt North-East, (KGW) Klinghardt West, (KKS1+2) Kaukausib South, (KKV1-3) Kaukausib Valley, (RK) Rotkuppe, (SD1+2) Sargdeckel;

**Succulent Karoo:** (BB) Boegoeberge, (BF1+2) Bogenfels, (HN) Holga North, (HOE) Höchster, (KGS1-4) Klinghardt South, (KGSW1+2) Klinghardt South-West, (KKS3) Kaukausib South, (KTV1+2) Kortdoornvlakte, (LUE) Lüderitz, (OD) Obib Dunes, (OM) Obib Mountains, (RDE) Red Dune East, (YD) Yellow Dune, (YDRD1+2) Yellow Dune Red Dune Transect.

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 Gariep 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



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