Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
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Observations on the diversity of termites in Angola and Namibia

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ABSTRACT

Termites are widely distributed, and the highest number of genera are documented for the Afrotropical region. Nevertheless, data or species lists for southern Africa were mainly compiled by a few scientists during several field surveys between the 1950s and 1970s. However, knowledge about the diversity and endemism of termites in highland areas was not collated during these surveys and has not been assembled to date. Since then, different scientists used these datasets to measure the species richness or the endemic species richness for single countries, e.g., South Africa. Termite species lists for Angola are scarce and were compiled for only a few regions, where 10 of 93 species were found to be endemic. Our current knowledge about the termite species diversity in Namibia is substantially better, with 8 of 54 species from four families being endemic. However, recent molecular studies on single termite species show high genetic diversity. More research on the currently available material in collections as well as molecular studies on species from southern Africa is needed.

Keywords: Angola, diversity, endemism, highlands, Namibia, termites

INTRODUCTION

Termites are eusocial insects systematically classified as roaches based on morphology, anatomy (Handlirsch 1903, 1904, Desneux 1904, Lameere 1909) and molecular studies (Lo *et al*. 2000, Inward *et al*. 2007b, Krishna *et al*. 2013). Within the roaches, termites belong to the epifamily Termitoidae; preferably, the term Isoptera is used as an unranked clade name (Krishna *et al*. 2013, Janion-Scheepers *et al*. 2016). The monogeneric family Cryptocercidae (genus *Cryptocercus*) is the sister group to the Isoptera (Eggleton 2001, Krishna *et al*. 2013). Approximately 3,000 extant termite species have been described worldwide in about 280 genera (Eggleton 2000, Kambhampati & Eggleton 2000, Uys 2002). Eggleton (2000) analysed the global termite diversity pattern and could show the highest value of genera in the Afrotropical region due to the high habitat diversity. Five termite families are represented by 54 genera in southern Africa, excluding Angola (Uys 2002). These values indicate that this region is rich in genera because the Termitidae originated in Africa (Bourguignon *et al*. 2016). The highest generic diversity of termites occurs in the Congolian rainforest (Jones & Eggleton 2010, Janion-Scheepers *et al*. 2016, Lind *et al*. 2022).

Termites alter their environment and soil properties by collecting litter, through their feeding behaviour as decomposers and due to their nest construction (Jones *et al*. 1994, Dangerfield *et al*. 1998, Sileshi *et al*. 2010, Juergens 2013, Jürgens *et al*. 2021). Additionally, they greatly impact nutrient cycling and plant species diversity (Donovan *et al*. 2001, Adams & Otárola-Castillo 2013, Erpenbach 2015, Jouquet *et al*. 2016, Wildermuth *et al*. 2021). Therefore, they are known as ecosystem engineers. Examples from southern Africa are *Macrotermes michaelseni* (Dangerfield *et al*. 1998, Wildermuth *et al*. 2021, 2022), *Psammotermes allocerus* (Juergens 2013) and *Microhodotermes viator* (McAuliffe *et al*. 2019).

TERMITE SPECIES DIVERSITY IN SOUTHERN AFRICA

The knowledge about termite families, genera and species in southern Africa, excluding Angola, was mainly gained between the 1950s and the 1970s (e.g., by Sands 1957, Coaton 1958, Williams 1966, Ruelle 1970, Coaton & Sheasby 1972, 1973). These publications were based on more than 35,000 samples from Namibia, South Africa, Zimbabwe and Eswatini (formerly Swaziland) (Uys 2002, Janion-Scheepers *et al*. 2016). The most detailed and comprehensive distribution maps, information about nest structures and biological observations were mainly collected and published by Coaton and Sheasby in national surveys of the Isoptera of southern Africa from 1973 to 1980 and published in the journal *Cimbebasia* (e.g., Coaton 1958, Coaton & Sheasby 1973, 1974, 1975, 1980). Mitchell (1980) published a survey of the termite diversity occurring in Zimbabwe. Uys (2002) compiled the documentation of 54 genera occurring in South Africa, Zimbabwe, Mozambique, Botswana, Eswatini, Lesotho and Namibia in her guide to termite genera. She identified 165 species in the 54 genera, of which 25% of the species could be endemic. The family Termitidae comprises the highest number of genera (Uys 2002).

These surveys did not collect data such as distribution maps or species diversity lists concerning termite endemics in highlands and escarpments of Angola and Namibia (the HEAN zone, Mendelsohn & Huntley 2023).

Research topics on termite phylogenies, reproductive biology, mound architecture, gut microbial communities and others were compiled by several scientists in different volumes (Krishna & Weesner 1969, 1970, Abe *et al*. 2000, Bignell *et al*. 2011). Krishna *et al*. (2013) arranged all termite species and their general distribution range in seven volumes, the 'Treatise on the Isoptera of the World'. A detailed termite literature list was published in subchapter 3.2.1 'Isoptera' by Janion-Scheepers *et al*. (2016).

Several scientists used the datasets from Coaton & Sheasby in the past. Zeidler (1997) investigated the distribution patterns of generic termite species richness from Namibia by implementing a Geographic Information System and could show that some species occur in specific annual precipitation ranges, e.g., *Psammotermes allocerus* occurs from 30 mm to 100 mm. The same dataset was recently used by Lind *et al*. (2022) to identify feeding groups of termites that consume wood, grass, detritus and soil organic material (Eggleton & Tayasu 2001) in relation to rainfall gradients in southern Africa.

From 2000 onwards, termite species richness was investigated in smaller study areas, e.g., by Zeidler *et al*. (2002). They investigated the diversity on five farms in southern Kunene Region of Namibia and could show a difference in diversity depending on the land-use intensity. Termites were also documented within the Biodiversity Monitoring Transect Analysis (BIOTA) in Africa project (Grohmann *et al*. 2010, Jürgens *et al*. 2010) on 45 sites from Namibia to South Africa. Schyra *et al*. (2018) investigated termite community structures from six sampling sites using phylogenetic analyses and revealed that species composition changes along a climate gradient. Other studies focused on single termite species regarding their spatial pattern (Grohmann *et al*. 2010, Wildermuth *et al*. 2021, 2022), nest structure (Tschinkel 2010), ecological relationships and fairy circles (Juergens 2013), physiology (Grube & Rudolph 1995), phylogenetic diversity (Gunter *et al*. 2022a, 2023, Jürgens *et al.* 2023) and morphological diversity (Gunter *et al*. 2022b).

The treatise by Krishna *et al*. (2013) and a few recently published data are the main sources for this paper.

TERMITE ENDEMISM IN ANGOLA AND NAMIBIA

Detailed biogeographical information on termite species that could be endemic in the HEAN zone is scant and can be obtained only by checking the literature by Krishna and colleagues (Krishna & Weesner 1969, 1970, Krishna *et al*. 2013) or the original maps published by Coaton and Sheasby (1972, 1973, 1974, 1975, 1980). The published maps by Coaton and Sheasby show that they are mainly focused on study sites near the main roads and do not focus on specific areas, e.g., highlands in Namibia (Coaton & Sheasby 1972). Therefore, information on the occurrence of termite species in the HEAN zone, as defined by Mendelsohn and Huntley (2023), was not mentioned.

Angola

Silvestri (1914) described the first termite observations for Angola near San Paolo de Loanda (Weidner 1956). Later, Weidner published three volumes about termite diversity in Angola (Weidner 1956, 1961, 1974). All information about species lists, morphology and nest descriptions are based on surveys by A de Barros Machado from the area of Dundo in northeast Angola. Weidner also compiled observations from other entomologists (e.g., M Burr) who stated that the most frequently encountered insects in the highlands (900–1,200 masl) are termites. Termites also occur on the highest mountains, first recorded during the Jessen survey in 1931–1932 (reported in Cosar 1934, Weidner 1956). Other authors who contributed to the study of these collections are Harris (1954), Noirot (1955), Emerson (in Weidner 1956) and de Carvalho (1971). Jürgens *et al*. (2021) recently discovered a new Hodotermitidae termite species in Angola; it is of an unknown genus, occurs mainly in the coastal region near the town of Baba and creates the largest known fairy circles (Jürgens *et al*. 2021).

In total, 93 species from three families – Hodotermitidae, Termitidae and Rhinotermitidae – are recorded and documented for Angola (Weidner 1956, 1961, 1974, Krishna *et al*. 2013, Jürgens *et al*. 2021). The family Termitidae presents the largest group and comprises 87 species from seven subfamilies. Only ten of 93 species are endemic to Angola (see Table 1). No other occurrences of these ten species are yet documented from other localities or countries. The endemics belong to the Hodotermitidae and three subfamilies of Termitidae. Molecular data have only been published for the Hodotermitidae (Jürgens *et al*. 2021), but not yet for the other nine species.

Namibia

The Namibian termite species are better documented and understood than Angola's termite diversity. The main fieldwork on species diversity in southern Africa was done by Coaton and Sheasby, as described above.

In Namibia, four termite families (Hodotermitidae, Kalotermitidae, Rhinotermitidae and Termitidae) are represented by 13 genera and at least 54 species, but only eight species were listed as endemic by Uys (2002) and Krishna *et al*. (2013). The eight species belong to three subfamilies of the Termitidae (see Table 2). The sand termite species *Psammotermes allocerus* occurs in southern Africa. However, recently published data show a high genetic diversity based on mitochondrial markers (Gunter *et al*. 2022a, 2023, Jürgens *et al.* 2023) and morphological diversity (Gunter *et al*. 2022b). The authors conclude that *P. allocerus* is a species complex. Some genetic groups occur only in Namibia (e.g., *P. allocerus* 'Northern Namib') based on the current dataset and the studied area. The other listed species occur in the western parts of Namibia and are not known to be endemic in the HEAN zone. To date, there are no molecular data available for these species.

COMPARISON OF TERMITE ENDEMISM

Detailed species lists for southern Africa exist only for Namibia and South Africa. These lists were mostly compiled over 25 years, from the 1950s to the 1970s. The species lists for Angola are based on only a few field studies, mainly around Dundo (Weidner 1956, 1961, 1974). In the following years, scientists used the datasets compiled by these individuals (e.g., Muller *et al*. 1997, Uys 2002, Lind *et al*. 2022). More information on endemics was compiled only for

Table 1: *Endemic termite species of Angola.*

Family	Subfamily	Species	Locality in Angola	Reference
Hodotermitidae		*Hodotermitidae* sp. nov.	Baba and Virei	Jürgens *et al*. (2021)
Termitidae	Cubitermitinae	*Basidentitermes trilobatus*	Luimbale	Krishna *et al*. (2013, p. 1907)
Termitidae	Cubitermitinae	*Crenetermes elongatus*	Type locality: Cameia	Krishna *et al*. (2013, p. 1910), Weidner (1974)
Termitidae	Cubitermitinae	*Crenetermes mandibulatus*	Type locality: “Vallée marécageuse de la rivière Chonga, affl. Lumege, 100 km à l’est de Vila Luso”	Krishna *et al*. (2013, p. 1910), Weidner (1974)
Termitidae	Apicotermitinae	*Hoplognathotermes angolensis*	Type locality: source of Cuílo River, 400 km SSE of Dundo, near Coemba	Krishna *et al*. (2013, p. 1394), Weidner (1974)
Termitidae	Cubitermitinae	*Noditermes angolensis*	Type locality: Alto Chicapa	Krishna *et al*. (2013, p. 1962), Weidner (1974)
Termitidae	Cubitermitinae	*Ophiotermes gracilis*	Alto Chicapa	Krishna *et al*. (2013, p. 1966), Weidner (1974)
Termitidae	Termitinae	*Pericapritermes machadoi*	Hoque	Krishna *et al*. (2013, p. 2294), Weidner (1974)
Termitidae	Cubitermitinae	*Thoracotermes grevillensis*	Type locality: Muquitixe	Krishna *et al*. (2013, p. 1982), Weidner (1974)
Termitidae	Apicotermitinae	*Trichotermes machadoi*	Type locality: Dundo	Krishna *et al*. (2013, p. 1421), Weidner (1974)

Table 2: *Endemic termite species of Namibia.*

Family	Subfamily	Species	Locality in Namibia	Reference
Termitidae	Macrotermitinae	*Microtermes dubius*	Namibia (Damaraland): Dornveld near Windhoek	Krishna *et al*. (2013, p. 1096)
Termitidae	Macrotermitinae	*Odontotermes fockianus*	Okahandja (29°59’S, 16°58’E)	Krishna *et al*. (2013, p. 1174)
Termitidae	Macrotermitinae	*Odontotermes okahandjae*	Okahandja (29°59’S, 16°58’E)	Krishna *et al*. (2013, p. 1240)
Termitidae	Macrotermitinae	*Odontotermes rehobothensis*	Rehoboth	Krishna *et al*. (2013, p. 1258)
Termitidae	Apicotermitinae	*Skatitermes psammophilus*	64.3 km ex Gobabis–Epukiro	Krishna *et al*. (2013, p. 1410)
Termitidae	Apicotermitinae	*Skatitermes watti*	96.5 km ex Rundu–Grootfontein	Krishna *et al*. (2013, p. 1411)
Termitidae	Cubitermitinae	*Lepidotermes amydrus*	64 km ex Windhoek–Göllschau crossroads	Krishna *et al*. (2013, p. 1954)
Termitidae	Cubitermitinae	*Unguitermes unidentatus*	40 km ex Rundu–Grootfontein	Krishna *et al*. (2013, p. 1987)
Rhinotermitidae	Psammotermitinae	*Psammotermes* species complex	Angola, Namibia, South Africa	Gunter *et al*. (2022a, 2023)

South Africa (Muller *et al*. 1997, Janion-Scheepers *et al*. 2016). Muller *et al*. (1997) used distribution maps of 25 species published by Coaton and Sheasby and reported that five of these 25 species are endemic to South Africa. Janion-Scheepers *et al*. (2016) analysed 39 genera and 126 species in South Africa, of which a third are said to be endemic.

The species lists and studies compiled to date indicate that further research in the field is needed to investigate the termite species diversity in Namibia and Angola. Additionally, more species from these countries should be included in molecular studies. This should be done especially for Angola, where only very few termite species have been investigated in molecular and phylogenetic studies, and further field surveys are necessary. Very few, if any, detailed distribution maps are available for the species mentioned in this study.

MOLECULAR STUDIES

Based on molecular studies, termites were grouped with roaches (Lo *et al*. 2000, Inward *et al*. 2007a, Legendre *et al*. 2008, Bourguignon *et al*. 2015). Only a few termite samples from southern Africa were used in molecular studies. Schyra *et al*. (2018) collected termites from five farms in central eastern Namibia and studied the termite community based on mitochondrial data and environmental factors. Gunter *et al*. (2022a, 2023) collected samples of sand termites, *P. allocerus*, at 113 study sites in Angola, Namibia and South Africa. The DNA (deoxyribonucleic acid) barcoding results found high genetic diversity, leading to the conclusion that *Psammotermes* is a species complex. Similar results were shown by others focusing on termite species from eastern Africa. Gunter *et al*. (2022b) could also show morphological differences within the sand termite complex that might show the sand termite to be more than one species. A new termite species for the Hodotermitidae was investigated in Angola with DNA barcoding and detailed morphological methods. These studies with these methods show that a revision of termite diversity in southern Africa, especially, is important. Janion-Scheepers *et al*. (2016) point to other termite genera, e.g., *Odontotermes* and *Microtermes*, that should be revised.

THREATS AND CONSERVATION

Currently, no termite species from southern Africa is listed on the IUCN (International Union for Conservation of Nature) Red List of threatened species. Based on the taxonomic status of the endemics, there is insufficient information and further research is essential.

CONCLUSION

As Janion-Scheepers *et al*. (2016) mentioned, future revisions of termite genera from southern Africa should first focus on current collections because there are thousands of unidentified samples. However, recent new sampling has helped with the molecular classification and determination of the genetic diversity of individual genera. A start was made by Gunter *et al*. (2022a, 2023). Additionally, modern measurement methods (geometric morphometrics, GMM) and digitisation can help to reclassify previous morphological determinations (Jürgens *et al*. 2021, Gunter *et al*. 2022a, 2022b, 2023, Jürgens *et al.* 2023). The literature review shows that Angola has the largest gap in termite sampling and knowledge of species diversity. To make additional statements about endemic occurrences of termites in southern Africa, further field studies need to be carried out.

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REFERENCES

Abe T, Bignell DE, Higashi M (eds) (2000) *Termites: evolution, sociality, symbioses, ecology*. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-017-3223-9.

Adams DC, Otárola-Castillo E (2013) Geomorph: an r package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution* 4(4): 393–399. https://doi.org/10.1111/2041-210X.12035.

Bignell DE, Roisin Y, Lo N (eds) (2011) *Biology of termites: a modern synthesis*. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-90-481-3977-4.

Bourguignon T, Lo N, Cameron SL, Šobotník J, Hayashi Y, Shigenobu S *et al.* (2015) The evolutionary history of termites as inferred from 66 mitochondrial genomes. *Molecular Biology and Evolution* 32(2): 406–421. https://doi.org/10.1093/molbev/msu308.

Bourguignon T, Lo N, Šobotník J, Ho SYW, Iqbal N, Coissac E *et al.* (2016) Mitochondrial phylogenomics resolves the global spread of higher termites, ecosystem engineers of the tropics. *Molecular Biology and Evolution* 34(3): 589–597. https://doi.org/10.1093/mol bev/msw253.

Coaton WGH (1958) The hodotermitid harvester termites of South Africa. *Science Bulletin* 375(43): 112. Department of Agriculture, Division of Entomology, Union of South Africa.

Coaton WGH, Sheasby JL (1972) Preliminary report on a survey of the termites (Isoptera) of South West Africa. *Cimbebasia Memoir Series* 2: 1–129.

Coaton WGH, Sheasby JL (1973) The genus *Psammotermes* Desneux (Rhinotermitidae). *Cimbebasia* 3(3): 19–28.

Coaton WGH, Sheasby JL (1974) The genus *Microhodotermes* Sjöstedt (Hodotermitidae). *Cimbebasia:* 3(6): 47–59.

Coaton WGH, Sheasby JL (1975) National survey of the Isoptera of southern Africa, 10: The genus *Hodotermes* Hagen (Hodotermitidae). *Cimbebasia* A(3): 105–138.

Coaton WGH, Sheasby JL (1980) National survey of the Isoptera of southern Africa, 18: the genus *Bifiditermes* Krishna (Kalotermitidae). Entomology Memoir, Department of Agricultural Technical Services, Republic of South Africa 53: 1–13

Cosar HG (1934) Die Termiten in der Afrikanischen Landschaft. *Beihefte zu den Mitteilungen der Geographischen Gesellschaft zu Rostock* 2: 1–85.

Dangerfield JM, Mccarthy TS, Ellery WN (1998) The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology* 14(4): 507–520. https://doi.org/10.1017/S0266467498000364.

De Carvalho J (1971) *Introdução à entomologia florestal de Angola*. Universidade de Luanda and Istituto de Investigação Agronomica de Angola, Nova Lisboa.

Desneux J (1904) A propos de la phylogénie des termitides. *Annales de la Société entomologique de Belgique* 48: 278–289.

Donovan SE, Eggleton P, Dubbin WE, Batchelder M, Dibog L (2001) The effect of a soil-feeding termite, *Cubitermes fungifaber* (Isoptera: Termitidae) on soil properties: termites may be an important source of soil microhabitat heterogeneity in tropical forests. *Pedobiologia* 45(1): 1–11. https://doi.org/10.1078/0031-4056-00063.

Eggleton P (2000) Global patterns of termite diversity. In: Abe T, Bignell DE, Higashi M (eds) *Termites: evolution, sociality, symbioses, ecology*. 25–51. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-017-3223-9.

Eggleton P (2001) Termites and trees: a review of recent advances in termite phylogenetics. *Insectes Sociaux* 48(3): 187–193. https://doi.org/10.1007/PL00001766.

Eggleton P, Tayasu I (2001) Feeding groups, lifetypes and the global ecology of termites: Ecology of termites. *Ecological Research* 16(5): 941–960. https://doi.org/10.1046/j.1440-1703.2001.00444.x.

Erpenbach A (2015) *Termite mounds as islands of diversity in West African savanna landscapes*. Doctoral thesis, Johann Wolfgang Goethe-Universität, Frankfurt am Main.

Grohmann C, Oldeland J, Stoyan D, Linsenmair KE (2010) Multi-scale pattern analysis of a mound-building termite species. *Insectes Sociaux* 57(4): 477–486. https://doi.org/10.1007/s00040-010-0107-0.

Grube S, Rudolph D (1995) Termites in arid environments: The waterbalance of *Psammotermes allocerus* Silvestri. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie* 10: 665–668.

Gunter F, Henschel JR, Picker MD, Oldeland J, Jürgens N (2022a) Phylogeny of sand termites. *Biodiversity & Ecology* 7: 51–54. https://doi.org/10.7809/b-e.00364.

Gunter F, Oldeland J, Henschel JR, Picker MD, Jürgens N (2022b) Not one but several: morphological diversity within the sand termite. *Biodiversity & Ecology* 7: 46–51. https://doi.org/10.7809/b-e.00363.

Gunter F, Oldeland J, Picker MD, Henschel JR, Jürgens N (2023) Cryptic subterranean diversity: regional phylogeography of the sand termite *Psammotermes allocerus* Silvestri, 1908 in the wider Namib region. *Organisms Diversity & Evolution* 23(1): 139–150. https://doi.org/10.1007/s13127-022-00580-w.

Handlirsch A (1903) Zur Phylogenie der Hexapoden. *Akademie der Wissenschaften in Wien* 112: 716–738.

Handlirsch A (1904) Zur Systematik der Hexapoden. *Zoologischer Anzeiger* 27(23–24): 733–759.

Harris W (1954) Exhibit of two nests of a species of *Apicotermes* from Angola. *Proceedings of the Royal Entomological Society of London* 19(7): 35.

Inward D, Beccaloni G, Eggleton P (2007a) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biology Letters* 3(3): 331–335. https://doi.org/10.1098/rsbl.2007.0102.

Inward DJG, Vogler AP, Eggleton P (2007b) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Molecular Phylogenetics and Evolution* 44(3): 953–967. https://doi.org/10.1016/j.ympev.2007.05.014.

Janion-Scheepers C, Measey J, Braschler B, Chown SL, Coetzee L, Colville JF *et al.* (2016) Soil biota in a megadiverse country: current knowledge and future research directions in South Africa. *Pedobiologia* 59(3): 129–174. https://doi.org/10.1016/j.pedobi.2016.03.004.

Jones DT, Eggleton P (2010) Global biogeography of termites: a compilation of sources. In: Bignell DE, Roisin Y, Lo N (eds) *Biology of Termites: a Modern Synthesis*.: 477–498. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-90-481-3977-4_17.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69(3): 373. https://doi.org/10.2307/3545850.

Jouquet P, Bottinelli N, Shanbhag RR, Bourguignon T, Traoré S, Abbasi SA (2016) Termites: the neglected soil engineers of tropical soils. *Soil Science* 181(3/4): 157–165. https://doi.org/10.1097/SS.0000000000000119.

Jürgens N (2013) The biological underpinnings of Namib Desert fairy circles. *Science* 339(6127): 1618–1621. https://doi.org/10.1126/science.1222999.

Jürgens N, Groengroeft A, Gunter F (2023) Evolution at the arid extreme: the influence of climate on sand termite colonies and fairy circles of the Namib Desert. *Philosophical Transactions of the Royal Society B* 378(1884): 20220149. https://doi.org/10.1098/rstb.2022.0149.

Jürgens N, Gunter F, Oldeland J, Groengroeft A, Henschel JR, Oncken I, Picker MD (2021) Largest on earth: discovery of a new type of fairy circle in Angola supports a termite origin. *Ecological Entomology* 46(4): 777–789. https://doi.org/10.1111/een.12996.

Jürgens N, Schmiedel U, Hoffman T (eds) (2010) *Biodiversity in southern Africa*. Klaus Hess Publishers, Göttingen.

Kambhampati S, Eggleton P (2000) Taxonomy and phylogeny of termites. In: Abe T, Bignell DE, Higashi M (eds) *Termites: evolution, sociality, symbioses, ecology*.: 1–23. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-017-3223-9_1.

Krishna K, Grimaldi DA, Krishna V, Engel MS (2013) Treatise on the Isoptera of the world: Volumes 1–7. *Bulletin of the American Museum of Natural History* 377(7): 1–2704. https://doi.org/10.1206/377.1.

Krishna K, Weesner F (1969) *Biology of termites.* Volume 1. Academic Press, New York.

Krishna K, Weesner F (1970) *Biology of termites.* Volume 2. Academic Press, New York.

Lameere A (1909) Assemblée générale du 26 Décembre 1909. *Annales de la Société Entomologique de Belgique* 53: 507–516.

Legendre F, Whiting MF, Bordereau C, Cancello EM, Evans TA, Grandcolas P (2008) The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear markers: implications for the evolution of the worker and pseudergate castes, and foraging behaviors. *Molecular Phylogenetics and Evolution* 48(2): 615–627. https://doi.org/10.1016/j.ympev.2008.04.017.

Lind BM, Uys VM, Eggleton P, Hanan N (2022) Precipitation mediates termite functional diversity and dominance in southern Africa. *Bothalia, African Biodiversity & Conservation* 52(1): 1–13. https://doi.org/10.38201/btha.abc.v52.i1.3.

Lo N, Tokuda G, Watanabe H, Rose H, Slaytor M, Maekawa K, Bandi C, Noda H (2000) Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Current Biology* 10(13): 801–804. https://doi.org/10.1016/S0960-9822(00)00561-3.

McAuliffe JR, Hoffman MT, McFadden LD, Jack S, Bell W, King MP (2019) Whether or not heuweltjies: context-dependent ecosystem engineering by the southern harvester termite, *Microhodotermes viator*. *Journal of Arid Environments* 163: 26–33. https://doi.org/10.1016/j.jaridenv.2018.11.012.

Mendelsohn JM, Huntley BJ (2023) Introducing the highlands and escarpments of Angola and Namibia. In: Mendelsohn JM, Huntley BJ, Vaz Pinto P (eds) Monograph on endemism in the highlands and escarpments of Angola and Namibia. *Namibian Journal of Environment* 8: 7–22.

Mitchell B (1980) *Report on a survey of the termites of Zimbabwe*. Unpublished report: National Museum and Monuments, Zimbabwe. pp. 1–135.

Muller C, Freitag S, Scholtz C, van Jaarsveld A (1997) Termite (lsoptera) distributions, endemism, species richness and priority conservation areas: consequences for land-use planning in South Africa. *African Entomology* 5(2): 261–271.

Noirot C (1955) Termites du centre et du sud-ouest de l'Angola récoltés par A. *Publicações Culturais da Companhia de Diamantes de Angola-Diamang* 27: 139–150.

Ruelle J (1970) Revision of the termites of the genus *Macrotermes* from the Ethiopian region (Isoptera: Termitidae). *Bulletin of the British Museum (Natural History) Entomology* 24: 363–444.

Sands W (1957) A revision of the East African Nasutitermitinae (Isoptera). *Bulletin of the British Museum (Natural History) Entomology* 5: 1–28.

Schyra J, Hausberger B, Korb J (2018) Phylogenetic community structure of southern African termites (Isoptera). *Sociobiology* 65(1): 15.

Sileshi GW, Arshad MA, Konaté S, Nkunika POY (2010) Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. *Journal of Vegetation Science* 21(5): 923–937. https://doi.org/10.1111/j.1654-1103.2010.01197.x.

Sivestri (1914) Contribuzione alla conscenza dei Termitidi e Termitofili dell'Africa occidentale. I. Termitidi. *Bollettino del Laboratorio di Zoologia Generale e Agraria della Reale Scoula Superiore d'Agricoltura, Portici* 9: 1–146.

Tschinkel WR (2010) The foraging tunnel system of the Namibian desert termite, *Baucaliotermes hainesi*. *Journal of Insect Science* 10(65): 1–17. https://doi.org/10.1673/031.010.6501.

Uys VM (2002) *A guide to the termite genera of southern Africa*. Plant Protection Research Institute, Agricultural Research Council, Pretoria.

Weidner H (1956) Beiträge zur Kenntnis der Termiten Angolas, hauptsächlich auf Grund der Sammlungen und Beobachtungen von A. de Barros Machado (I. Beitrag). *Publicações Culturais da Companhia de Diamantes de Angola-Diamang* 29: 55–106.

Weidner H (1961) Beiträge zur Kenntnis der Termiten Angolas, hauptsächlich auf Grund der Sammlungen und Beobachtungen von A. de Barros Machado (2. Beitrag). *Publicações Culturais da Companhia de Diamantes de Angola-Diamang* 54: 13–77.

Weidner H (1974) Beiträge zur Kenntnis der Termiten Angolas, hauptsächlich auf Grund der Sammlungen und Beobachtungen von A. de Barros Machado (3. Beitrag). *Publicações Culturais da Companhia de Diamantes de Angola-Diamang* 88: 13–78.

Wildermuth B, Oldeland J, Arning C, Gunter F, Strohbach B, Juergens N (2022) Spatial patterns and life histories of *Macrotermes michaelseni* termite mounds reflect intraspecific competition: insights of a temporal comparison spanning 12 years. *Ecography* 2022(9). https://doi.org/10.1111/ecog.06306.

Wildermuth B, Oldeland J, Juergens N (2021) A beneficial relationship: associated trees facilitate termite colonies (*Macrotermes michaelseni*) in Namibia. *Ecosphere* 12(7). https://doi.org/10.1002/ecs2.3671.

Williams RMC (1966) The East African termites of the genus *Cubitermes* (Isoptera: Termididae). *Transactions of the Royal Entomological Society of London* 118: 73–118.

Zeidler J (1997) *Distribution of termites (Isoptera) throughout Namibia – environmental connections*. PhD thesis, University of the Witwatersrand, Johannesburg.

Zeidler J, Hanrahan S, Scholes M (2002) Termite species richness, composition and diversity on five farms in southern Kunene region, Namibia. *African Zoology* 37(1): 7–11. https://doi.org/10.1080/15627020.2002.11657148.