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Doctor of Philosophy

**Worldwide Historical Biogeography of Termites (Blattodea: Isoptera)**

Submitted by: Menglin Wang  
Supervised by: Thomas Bourguignon  
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## Declaration of Original Authorship

### Declaration of Original Authorship

I, Menglin Wang, declare that the thesis entitled “Worldwide historical biogeography of termites (Blattodea: Isoptera)” and the data presented in it are original and my own work.

I confirm that:

- No part of this work has previously been submitted for a degree at this or any other university.
- References to the work of others have been clearly acknowledged. Quotations from the work of others have been clearly indicated, and attributed to them.
- In cases where others have contributed to part of this work, such contribution has been clearly acknowledged and distinguished from my own work.
- None of this work has been previously published elsewhere, with the exception of the following:
  1. Wang, M., A. Buček, J. Šobotník, D. Sillam-Dussès, T. A. Evans, Y. Roisin, N. Lo, and T. Bourguignon. 2019. Historical biogeography of the termite clade Rhinotermitinae (Blattodea: Isoptera). *Molecular Phylogenetics and Evolution* 132:100–104.

Name: Menglin Wang

Signature: 王梦琳

Date: 2021. 12

## **Abstract**

Termites are of crucial importance in terrestrial tropical and subtropical ecosystems where they play a key role in organic matter decomposition. Termites descent from a wood-feeding cockroach ancestor and diverged from the subsocial wood roach *Cryptocercus* more than 150 million years ago. Given that the origin of termites predates the breakup of the Pangaea, termites potentially acquired their current distribution pattern by a combination of vicariance, through continental drift, or oceanic dispersal, through over-water rafting or land bridges. The origin of termite distribution, called historical biogeography, can be studied by mean of reconstruction of ancestral distribution on time-calibrated phylogenetic trees. Although several studies have already reconstructed the global historical biogeography of termite lineages within the Neoisoptera, these studies did not investigate non-Neoisoptera termites and overlooked one biogeographic realm with unique fauna, Madagascar. In this project, I used complete mitochondrial genomes to build time-calibrated phylogenetic trees of termites and determine the precise dispersal events of yet unstudied termite lineages to and of yet unstudied biogeographic realms. I sequenced the mitochondrial genomes of about 2500 samples including almost all termite species from North, South, and Central America and representatives of the termite diversity from Madagascar. In the chapters 1 and 2, I resolved the historical biogeography of Rhinotermitinae and the early-branching termite families Hodotermitidae, Stolotermitidae, and Archotermopsidae. In the chapter 3, I resolved the historical biogeography of termites from Madagascar. And in the chapter 4, I produced a near-complete phylogenetic tree of termites from the Americas that I used to study the diversification patterns of termites across the two continents that composed the New World. My thesis sheds light on the historical biogeography of termites at the global scale.

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## **List of Publications**

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## **Contributions**

M.W. handled the all data analysis, wrote the manuscript, conducted the research experiment.

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## **Introduction**

### **Diversity and distribution of the main termite families**

Termites are generally regarded as pest by the public, unaware of the crucial role they play in plant organic matter decomposition, soil bioturbation, and soil nutrient cycling (Su and Scheffrahn 2000, Jones and Eggleton 2011, Jouquet et al. 2016). Previous studies have estimated that termite activities cost 32 billion dollars every year, pushing many researchers to elaborate pest control strategies relying on both chemical and biological approaches (Rust 2014, Su 2019). However, a minority of termite species are wood-feeders, while the majority of species feed on other types of organic matter substrates, such as soil organic matter (Donovan et al. 2001; Krishna et al. 2013). Traditionally, termites are divided into two groups: the paraphyletic “lower” termites, which mainly feed on wood and host protozoa helping them to digest lignocellulose in their guts; and the “higher” termites, which feed on substrates scattered along the wood-soil decomposition gradient and lost their gut protozoa (Vinet and Zhedanov 2010, Brune 2014). While all lower termites are wood-feeders (or exceptionally grass-feeders, like the Hodotermitidae) and are assigned feeding group I, the higher termites feed on comparatively more diverse substrates. Higher termites are classified into three feeding groups: the feeding group II includes all species of Termitidae feeding on wood, leaf litter, and grass, as well as the fungus-growing Macrotermitinae (which are sometime classified in a separate feeding group III); the feeding-group III includes the termitids that feed on soil rich in organic-rich matter and are usually active at the wood-soil interface; the feeding-group IV includes species of Termitidae that feed on soil with lower organic matter content and are usually regarded as true soil-feeders (Donovan et al. 2001, Jones and Eggleton 2011). Termites, and more particularly Termitidae, reach their highest richness in tropical and subtropical terrestrial ecosystems, making up 10-20% of the animal biomass in these regions, a high abundance that is explained by the abundance of their food and the diversity of their feeding habits (Jones and Eggleton 2011, Bourguignon et al. 2015).

Previous time-calibrated phylogenetic trees showed that termites diverged from their sister group, the wood roach *Cryptocercus*, 170 million years ago (Ma) (Bourguignon et al. 2015, Bucek et al. 2019). The most recent common ancestor of modern termites was estimated at ~140 Ma, implying that termite’s origin predates the final stage of the breakup of Pangaea (Bourguignon et al. 2015, Bucek et al. 2019). The distribution of the first termites may therefore be explained by continental drift. Based on both molecular and morphological evidences, Mastotermitidae has been unambiguously retrieved as the most ancestral termite family, forming the sister group of all other modern termites (Lo et al. 2000, Inward et al. 2007b, Legendre et al. 2008, Cameron et al. 2012, Bourguignon et al. 2015, Bucek et al. 2019). Many Mastotermitid fossils have been found around the world, including in Russia, South America, Africa, Europe, and South Asia. However, the only living species, *Mastotermes darwiniensis*, occurs in northern Australia and southern New Guinea, where it was introduced (Krishna and Emerson 1983, Krishna and Grimaldi 1991, Vršanský and Aristov 2014, Engel et al. 2015, Zhao et al. 2019a, Bezerra et al. 2020). Taken together, these observations suggest that the distribution of Mastotermitidae may have been influenced by vicariance through continental drift. However, this hypothesis cannot be tested in a molecular framework given the absence of modern species of Mastotermitidae other than *M. darwiniensis*. In contrast, other termite families are represented by a larger number of modern species, allowing to determine the factors at the origin of their modern distribution.

The second split within the phylogenetic tree of modern termites separates a clade composed of Stolotermitidae, Hodotermitidae, and Archotermopsidae from Neoisoptera + Kalotermitidae. The phylogenetic relationships among species and genera of Stolotermitidae, Hodotermitidae, and Archotermopsidae remain unclear because of partial sampling.

Bourguignon et al. (2015) retrieved the monophyletic Stolotermitidae as the sister group of Archotermopsidae + Hodotermitidae, with Hodotermitidae monophyletic and nested within the paraphyletic Archotermopsidae. The origin of these three families is not adequately reconstructed with currently available morphological and molecular phylogenies (Bourguignon et al. 2015). The most recent common ancestor of this group was estimated at 115 Ma by Bourguignon et al. (2015), prior to the final stage of the breakup of Pangaea, indicating that vicariance may have played a role in shaping their current distribution. The fossil record is fragmentary and provides little information about the past distribution of the group. Living Stolotermitidae showed a typical Gondwanan distribution across Australia, South Africa, South America, Tasmania, and New Zealand (Emerson and E. 1955, Gay and Calaby 1969, Kaulfuss et al. 2010). Living species of Hodotermitidae occur in the Ethiopian and Oriental regions, so well as in Iran and Pakistan (Krishna et al. 2013). The most recent common ancestor of *Microhodotermes*, *Zootermopsis*, and *Hodotermopsis* was estimated at 92 Ma, during the last stage of the breakup of Pangaea, making vicariance-driven distribution a possibility (Bourguignon et al. 2015). Living *Zootermopsis* occurs in western North America and was introduced in Japan, *Archotermopsis* is found in North India, Pakistan, and the Oriental region, while *Hodotermopsis* is endemic to the Oriental realm (Krishna et al. 2013). Altogether, the distribution of Stolotermitidae, Hodotermitidae, and Archotermopsidae, and their age estimation raises the possibility that their modern distribution was shaped by continental drift. This hypothesis can be studied using time-calibrated phylogenetic trees reconstructing the historical biogeography of the group.

Kalotermitidae is the most diverse termite family other than Termitidae (Krishna et al. 2013). All species of Kalotermitidae feed on wood, either sound or slightly decayed, and seldomly go out of their wood shelter to forage (Donovan et al. 2001, Abe 1987). The entire colony usually lives in a single piece of wood such as a dead branch on a standing tree. Kalotermitidae consists of 23 described extant genera, 466 living species, eight fossil genera, and 33 fossil species (Constantino 2016). The most famous species of Kalotermitidae is perhaps *Cryptotermes brevis*, a widely distributed species and one of the most important pests of timber (Scheffrahn et al. 2009, Evans et al. 2013). Fossil kalotermitids are present in amber of the Burmese, Baltic, and Dominican deposits (Krishna et al. 2013). Time-calibrated phylogenies estimated that Kalotermitidae split up from Neoisoptera ~120 Ma, before the breakup of Gondwana, indicating continental drift possibly shaped the distribution of early-diverging modern Kalotermitidae lineages (Bourguignon et al. 2015). As other wood-feeding termites, kalotermitids are also good dispersers, presumably able to sustain transoceanic dispersal rafting in their piece of wood. One argument supporting their high dispersal ability is their high salinity tolerance, suggesting they can survive transoceanic journey hidden inside their wood shelter (Chiu et al. 2021).

Stylotermitidae is a small monotypic family including the genus *Stylotermes* (Holmgren and Holmgren 1917). Mitochondrial genome and transcriptome phylogenies indicated that Stylotermitidae form the sister group of all other Neoisoptera (Wu et al. 2018, Bucek et al. 2019). Living *Stylotermes* are present in South and Southeast Asia, living and feeding on living trees. The Stylotermitidae have not been studied in details and our understanding of their biology is limited (Chhotani 1983, Liang et al. 2017).

The small family Serritermitidae is strictly Neotropical and include two genera, *Glossotermes* and *Serritermes*, and three species. The family is monophyletic and is nested within the paraphyletic Rhinotermitidae (Krishna et al. 2013, Bourguignon et al. 2015). *Serritermes* live in the mounds of *Cornitermes* (Termitidae, Syntermitinae) (Emerson and Krishna 1975) and *Glossotermes* is generally found in dead standing logs (Bourguignon et al. 2009). Rhinotermitidae is a polyphyletic assemblage, within which the Serritermitidae Termitidae are nested (Bourguignon et al. 2015, Bucek et al. 2019). Rhinotermitidae

includes 12 genera and 315 living species, distributed across all landmasses between 45°N and 45°S of latitude (Krishna et al. 2013, Constantino 2016). Among the Rhinotermitidae, the clade comprising *Coptotermes*, *Heterotermes*, and *Reticulitermes*, which forms the sister group of Termitidae, includes the termite species amongst the most intensively studied owing to their pest status (Su and Scheffrahn 2000). The most recent common ancestor of this clade was estimated at 59.5 Ma, indicating that they acquired their current distribution via both transoceanic and land bridge dispersals, so well as through human-mediated introduction (Bourguignon et al. 2016). Other lineages within the Rhinotermitidae similarly originated after the breakup of Pangaea, but have not been studied in details yet. This is the case of the pantropical Rhinotermitinae, whose distribution remains to be studied using time-calibrated phylogenetic trees.

Termitidae is the most speciose family of termites and comprises eight subfamilies, 256 genera, and 2110 species (Krishna et al. 2013, Constantino 2016). Termitidae, therefore, include two-thirds of termite species. Unlike wood-feeding lower termites, termitids feed on a diverse array of organic materials, including lichens, rotten wood, or soil organic matter (Bignell 2006, Jouquet et al. 2011, 2016). The loss of gut protists may have triggered the diet diversification observed in Termitidae (Noirot 1995). Termitidae are one of the major organic matter decomposers in tropical and subtropical terrestrial areas. Their historical biogeography has been studied in details previously (Bourguignon et al. 2017). Modern Termitidae originated in Africa and dispersed out-of-Africa since the end of the Eocene, ~34 Ma, following the global cooling the Earth experienced at the Eocene Oligocene boundary (Zachos et al. 2001).

Termites can be found on all continents except for the Antarctic, and their current distribution potentially can be explained by vicariance and dispersal events. Previous time-calibrated tree showed termite originated 150-170Ma (Bourguignon et al. 2015, Bucek et al. 2019), corresponding to the geological period when continents were connected (the Pangaea) which split up (the Laurasia and Gondwana supercontinents) later and subsequently formed the current continents (Scotese 2004). Hence, the current distribution of early diverged termites can potentially be explained by the continental drifts, with dispersal could not being ignored. Many studies focusing on the distribution of termites have been done using various biogeography reconstruction methods, including but not limited to RASP (Reconstruct Ancestral State in Phylogenies), APE package, and BioGeoBears in R (Matzke 2013, Paradis et al., 2004, Yu et al. 2015). Time-calibrated phylogenies have shown many termites groups dispersed via oversea rafting or land bridges. For example, Termitidae originated 42-54 Ma postdating the breakup of Pangaea and Gondwana. In addition, termites are weak in flight. Thus, the higher termites may acquire their current distribution via transoceanic dispersal or land bridges (Bourguignon et al. 2015). Similar patterns can also be found in most of the kalotermitids (Bucek et al. 2021, unpublished data)

### **Phylogenetic Relationship among Termite Lineages**

Compared with other hyper-diverse insect groups (e.g. Coleoptera and Hymenoptera), termites form a relatively small group of insects, only consisting of ~300 genera and ~3000 described species classified in nine extant families: Mastotermitidae, Hodotermitidae, Stolotermitidae, Archotermopsidae, Kalotermitidae, Stylotermitidae, Serritermitidae, Rhinotermitidae, and Termitidae (Krishna et al. 2013). Termites have a near-global distribution, as they are found on all emerged lands between 45°N and 45°S of latitude (Jones and Eggleton 2011, Krishna et al. 2013). They are, therefore, present on all continents but Antarctica.

The phylogenetic position of many termite genera remains unknown due to the lack of molecular data. The origin and the possible dispersal routes of many termite lineages also remain ambiguous because of partial sampling. However, we now have a good understanding of interfamilial relationships thanks to phylogenetic studies relying on comprehensive sampling of the termite tree of life and large molecular datasets, whose generation has been made possible by the rapid progress of sequencing technology. These phylogenies indicate that termites from the sister group of subsocial wood-feeding cockroaches *Cryptocercus* (Lo et al. 2000, Inward et al. 2007b, Legendre et al. 2008, Cameron et al. 2012, Bourguignon et al. 2015, Bucek et al. 2019) (Figure 1). *Cryptocercus* have similar gut protists to termites, and share two symplesiomorphies with *Mastotermes*: large anal lobes and two-lined egg ootheca (Nalepa and Lenz 2000, Engel et al. 2009).

The mitochondrial genome is a highly conserved DNA sequence that has been widely used to reconstruct phylogenetic relationships among lineages of insects (Gray 2012, Cameron 2014b). Mitochondrial genomes are A+T-rich genomes of bacterial origin containing a reduced number of genes (Cameron 2014a). The termite mitochondrial genome includes a control region and 37 genes, including 13 protein-coding genes, two ribosomal RNA genes, and thirteen transfer RNA genes (Cameron and Whiting 2007, Cameron et al. 2012). Initially, only morphological characters were used to reconstruct termite phylogeny (Donovan et al. 2000). Subsequent phylogenies were based on nuclear gene and mitochondrial gene fragments and significantly improved our understanding of the relationships among the main termite lineages (Lo et al. 2000, Inward et al. 2007, Legendre et al. 2008). These phylogenies, however, provided low support for some key nodes. With the development of new sequencing technologies and reduction of sequencing costs, complete mitochondrial genomes became relatively easy to sequence and widely used for phylogenetic reconstruction (Cameron et al. 2012, Bourguignon et al. 2015). Recently, phylogenies have been generated from larger molecular datasets, including termite transcriptomes, which have allowed researchers to reconstruct phylogenetic trees using a large number of molecular markers (Bucek et al. 2019). Ultra-Conserved Elements (UCEs) have also been developed for termites and provide a new way to build phylogenetic trees based on many markers at a low cost (Hellemans et al. *unpublished data*).

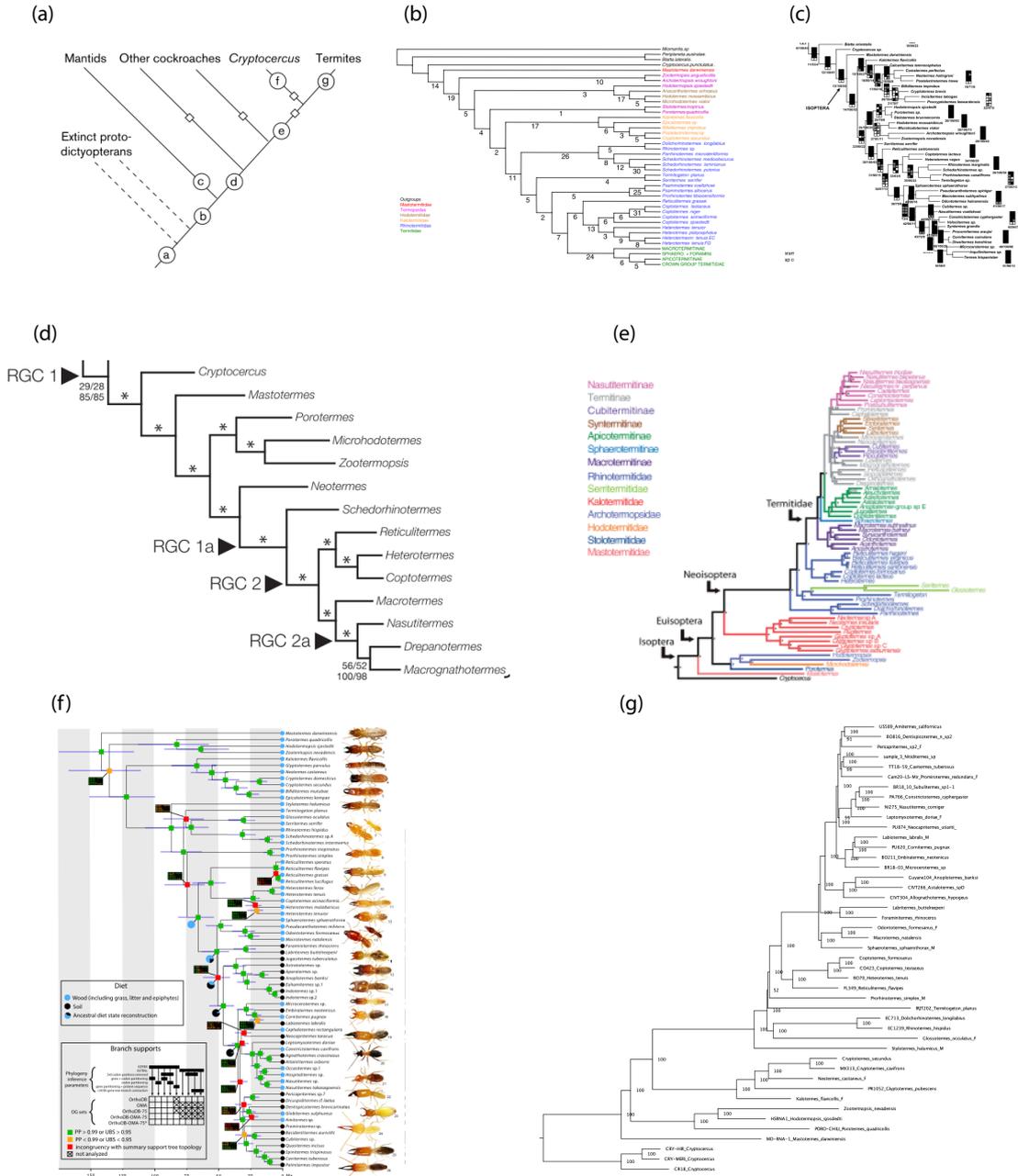
The relationship among the main termite lineages are now well resolved (Figure 1). Mastotermitidae diverged early and form the sister group to Euisoptera, a termite clade consisting of Stolotermitidae, Hodotermitidae, and Archotermopsidae, Kalotermitidae and Neoisoptera. Stolotermitidae, Hodotermitidae, and Archotermopsidae form a clade sister to all remaining Euisoptera. Within Stolotermitidae, both *Porotermes* and *Stolotermes* are monophyletic. Hodotermitidae is monophyletic and nested within Archotermopsidae, making it paraphyletic. All hodotermitid and archotermopsitid genera are monophyletic. Kalotermitidae is monophyletic and form the sister group of Neoisoptera, which consists of Rhinotermitidae, Stylotermitidae, Serritermitidae, and Termitidae. Rhinotermitidae is polyphyletic, with Heterotermittinae and *Coptotermes* clustering together and forming the sister group of Termitidae. Termitidae is monophyletic, and all subfamilies within

Termitidae are monophyletic, except for polyphyletic Termitinae (Lo et al. 2000, Inward et al. 2007, Legendre et al. 2008, Cameron et al. 2012, Bourguignon et al. 2015, Bucek et al. 2019).

Figure 1 Phylogenetic relationships among termites families and subfamilies (Blattodea: Isoptera).

(a) Key innovations during Termitoidae evolution. e: acquisition of gut protists; g: emergence of eusociality (adapted from Lo et al 2000). (b) Phylogeny of Inward et al. (2007) inferred with both morphological and molecular data. (c) Phylogenetic relationships among termites inferred from seven gene fragments (Legendre et al. 2008). (d) Phylogenetic tree based on the complete mitochondrial genomes with third codon positions excluded (Cameron et al. 2012). (e) Phylogenetic relationships among the main termite groups reconstructed using full mitochondrial genome (Bourguignon et al. 2015). (f) Maximum likelihood phylogeny inferred from termite transcriptomes (Bucek et al. 2019). (g) Phylogenetic tree reconstructed with 5,934 Ultra Conserved Elements (UCEs) which are specifically designed for termites by Dr. Hellemans (unpublished data).

# Introduction | Phylogenetic relationship among termite lineages



## **Evolution and Diversification of Termites**

Termites consist of ~3000 described species whose taxonomy and distribution have been reasonably well documented (Jones and Eggleton 2010, Krishna et al. 2013). Previous studies showed termites evolved from subsocial wood-feeding cockroaches ~150Ma and “higher” termites (Termitidae) arose ~50 Ma (Bourguignon et al. 2015, 2017, Bucek et al. 2019). “Lower” termites primarily feed on wood, relying on gut protists (Vinet and Zhedanov 2010, Brune 2014). The high species richness of Termitidae might be linked to the loss of protists in their gut that fostered new, unique, feeding habits, including diet made of leaf litter, moss, organic-rich soil, as well as fungus cultivation (Bourguignon et al. 2017, Chouvenc et al. 2021). Previous studies showed termite diverse feeding habits may have promoted their diversification (Davis et al. 2009, Legendre and Condamine 2018, Condamine et al. 2020).

Adaptive radiations are lineages experiencing rapid speciation for various reasons, such as the acquisition of new traits or the demise of competitors following major environmental changes (Schluter 2001, Yoder et al. 2010, Glor 2010, Myers and Burbrink 2012). Indeed, the evolution of innovations can trigger speciation and promote adaptive radiation by providing access to new ecological resources, increasing fitness and competitive strength of the innovation carriers (Simpson 1944, Heard and Hauser 1995). Termites are among the most abundant insects in the soil and wood of tropical and subtropical ecosystems where they reach their highest richness and have experienced adaptive diversification events (Jones and Eggleton 2010, Krishna et al. 2013). Species diversification can be studied by inferring the rates of speciation, extinction, and immigration using time-calibrated trees. Note, however, that it is debated whether diversification models are able to decompose the diversification rates measurable from time-calibrated trees into their two components, speciation rates and extinction rates (Louca and Pennell 2020, 2021). To date, there has been a handful of studies focusing on the processes that drove termite diversification using systematic analyses (Wilson 1992, Davis et al. 2009, Legendre and Condamine 2018, Condamine et al. 2020). These studies have hypothesized that termites experienced rapid speciation in two stages: following the rise of eusociality and following the loss of cellulolytic protists in the gut of Termitidae. The analyses of Legendre et al. (2018) suggested that speciation rate is higher in termite species with true workers than in termite species without true workers. The loss of protozoa in Termitidae is another key innovation that probably drove the diversification of Isoptera (Chouvenc et al. 2021). The transition from a diet made of wood digested with the assistance of gut protists to diverse feeding habits exclusively assisted with symbiotic gut bacteria and archaea possibly fostered the rapid diversification of Termitidae (Bourguignon et al. 2017, Chouvenc et al. 2021).

## **Aim of this thesis**

While the mechanisms of termite dispersal have been well documented for a couple of lineages, the historical biogeography of some termite lineages has not been studied in details yet. This is especially true for lineages that live in periphery of the termite centers of diversity, such as the Archotermopsidae, Hodotermitidae, and Stolotermitidae. Species in these families typically live in regions where few other termite species are found, and for these reasons have been poorly sampled. The historical biogeography of the family Kalotermitidae has not been studied in detail neither. Kalotermitidae are diverse and found around the world, but they are often difficult to collect, sometime living high up in the canopy of tropical forests, preventing easy sampling (Roisin et al. 2006). In this thesis, I reconstructed robust time-calibrated phylogenetic trees of the termite lineages that have not been studied in details yet. I used these trees to shed light on the historical biogeography of yet poorly studied termite lineages.

I also attempted to reconstruct a complete phylogenetic tree of termites from two biogeographic regions: the Neotropical and the Nearctic regions. A few studies have investigated the diversification processes of termites using phylogenetic trees (Davis et al. 2009, Legendre and Condamine 2018, Condamine et al. 2020). However, these studies are based on incomplete, fragmentary, phylogenetic trees, which make estimations of diversification rates (or speciation and extinction rates) unconvincing. Inevitably, the phylogenetic tree of termites from the Neotropical and Nearctic regions I produced is not complete, but the large sampling covering the entire distribution of termites in these two biogeographic regions is unparalleled by previous studies and allows me to refer to my tree as a near-complete phylogenetic tree of American termites. My phylogenetic tree shed light on the evolution of termites in the Americas. Using this phylogenetic tree, I intend in the future to study how termites have diversified in these continents

## **Chapter 1 Historical biogeography of the termite clade (Rhinotermitinae)**

(Published in Molecular Phylogenetics and Evolution as “Historical biogeography of the termite clade Rhinotermitinae (Blattodea: Isoptera)”)

The historical biogeography of Rhinotermitinae has already been published (Wang et al. 2019). Wang, M., A. Buček, J. Šobotník, D. Sillam-Dussès, T. A. Evans, Y. Roisin, N. Lo, and T. Bourguignon. 2019. Historical biogeography of the termite clade Rhinotermitinae (Blattodea: Isoptera). *Molecular Phylogenetics and Evolution* 132:100–104.

### **1.1 Introduction**

Monophyletic Rhinotermitinae is the sister group of all other Rhinotermitidae species with the most recent common ancestor estimated at 43 Ma (32–54Ma 95% HPD) (Lo et al. 2004, Austin et al. 2004, Inward et al. 2007, Bourguignon et al. 2015). Hence, dispersal is the only explanation of their current distribution. The phylogenetic position of *Parrhinotermes* remains unclear, either grouping with *Schedorhinotermes*, or forming the sister group of all other remaining Rhinotermitinae species. To shed light on the historical biogeography of Rhinotermitinae, I reconstructed a time-calibrated phylogeny with 27 mitochondrial genomes of this group and 11 fossils used as time constraints.

### **1.2 Published Article**

The historical biogeography of Rhinotermitinae has already been published (Wang et al. 2019).

Wang, M., A. Buček, J. Šobotník, D. Sillam-Dussès, T. A. Evans, Y. Roisin, N. Lo, and T. Bourguignon. 2019. Historical biogeography of the termite clade Rhinotermitinae (Blattodea: Isoptera). *Molecular Phylogenetics and Evolution* 132:100–104.

### **1.3 Conclusion**

Our analyses support the monophyly of Rhinotermitinae and all genera of Rhinotermitinae. The molecular clock trees provided time estimations that diverged by up to 15.6 million years depending on whether or not 3rd codon positions were included. Rhinotermitinae arose 50.4–64.6 Ma (41.7–74.5 Ma 95% HPD), showing that the Rhinotermitinae acquired their distribution through a combination of transoceanic dispersals and dispersals across land bridges. Because of the large intervals of the age estimations and the uncertainties of ancestral range reconstructions we could not draw final conclusions on the dispersal events. Although the sequencing of more samples, for example of the Neotropical *Acorhinotermes* and the Oriental *Macrorhinotermes*, are needed to draw a more complete picture of the historical biogeography of Rhinotermitinae, our phylogenetic analyses revealed the role played by long-distance over-water dispersal on the global distribution of modern termites.

## Chapter 2 Historical biogeography of early-diverging termite lineages (Blattodea: Termitoidea)

### 2.1 Introduction

Termites are a clade of social cockroaches forming a sister group with the wood-feeding cockroach genus *Cryptocercus* (Lo et al. 2000, Inward et al. 2007a, 2007b). The fossil record of termites dates back to the Early Cretaceous, ~130 Ma (Thorne et al. 2000b, Engel et al. 2016), and time-calibrated phylogenetic trees suggest that the first termites appeared 140-150 million years ago (Ma) (Engel et al. 2009, 2016, Legendre et al. 2015, Bourguignon et al. 2015, Bucek et al. 2019). Therefore, the origin of termites predates the final stage of the breakup of the Pangaea, and early-diverging termite lineages may have distribution patterns bearing the signature of vicariance through continental drift.

The first divergence amongst modern termites is that of Mastotermitidae and Euisoptera, the clade composed of all non-mastotermitid termites, ~140-150 Ma (Inward et al. 2007b, Engel et al. 2009, Bourguignon et al. 2015, Bucek et al. 2019). The only living species of Mastotermitidae, *Mastotermes darwiniensis*, is native to northern Australia and was introduced in New Guinea (Handel et al. 2016). However, fossils of *Mastotermes* have been unearthed in Russia, Mexico, the Dominican Republic, Brazil, Europe, Ethiopia, and Myanmar (Krishna and Emerson 1983, Krishna and Grimaldi 1991, Vršanský and Aristov 2014, Engel et al. 2015, Zhao et al. 2019a, Bezerra et al. 2020), indicating that *Mastotermes* was once globally distributed and acquired its modern relictual distribution through multiple extinction events. The past global distribution of *Mastotermes* can be explained by a combination of vicariance through continental drift and transoceanic dispersal events, in proportions that remain unclear. The discovery of new fossils may favor one scenario over the other. Another method, molecular-based time-calibrated phylogenetic trees, cannot be used in the case of the monotypic *Mastotermes*, but can be used to resolve the origin of the distribution patterns of other early-diverging termite lineages with broader extant distributions.

The first divergence within the Euisoptera is that of Stolotermitidae + Hodotermitidae + Archotermopsidae with Neoisoptera + Kalotermitidae dated at 130-145 Ma (Bourguignon et al. 2015, Bucek et al. 2019). The most recent common ancestor of the former clade corresponds to the split between Stolotermitidae and Archotermopsidae + Hodotermitidae and was estimated at 80-115 Ma (Ma, 95% HPD) (Bourguignon et al. 2015, Bucek et al. 2019). Therefore, cladogenesis in Stolotermitidae + Hodotermitidae + Archotermopsidae was initiated before the final stage of the breakup of Pangaea, indicating their current distribution may have been shaped by vicariance through continental drift (Bourguignon et al. 2015). Alternatively, despite their ancient origin, Stolotermitidae + Hodotermitidae + Archotermopsidae may have acquired their modern distribution pattern by dispersals, as shown for many animal taxa such as ratite birds (Phillips et al. 2010) and cichlids (Friedman et al. 2013). A comprehensive phylogenetic tree including samples collected across the distribution range of these three early-diverging termite families could help determine whether the modern distribution of early-diverging termite lineages was shaped by dispersal or vicariance.

Living Stolotermitidae are found in Australia, South Africa, South America, and New Zealand, a distribution often interpreted as relictual of a past distribution across Gondwana before the continent broke up some 100 Ma (Krishna et al. 2013). Modern Hodotermitidae are patchily distributed across the dry biomes found in Africa, the Middle East, and South Asia, a distribution they possibly acquired as grassland expanded following the global

cooling of the Eocene-Oligocene boundary, ~34 Ma (Zachos et al. 2001), during the Oligocene and Miocene (Krishna et al. 2013). And the Archotermopsidae have a disjunct distribution across the Northern hemisphere, with *Archotermopsis* living at the foothill of the Himalayan region and in Vietnam, *Hodotermopsis* living in Vietnam, South China, and Japan, and *Zootermopsis* occurring in western United States (Krishna et al. 2013). While the fossil record of the three families is more fragmentary than that of Mastotermitidae, some fossils are indicative of a wider past distribution. For example, *Cosmotermes*, a genus attributed to stotermitids (but see Jiang et al. 2021), is known from the Burmese amber (Zhao et al. 2019b), and *Termopsis*, a genus allied to Archotermopsidae + Hodotermitidae, is known from the Baltic amber (Krishna et al. 2013). The historical biogeography of Stotermitidae + Hodotermitidae + Archotermopsidae may thus be more intricate than previously acknowledged.

While the historical biogeography of Neoisoptera and Kalotermitidae has been studied in detail (Bourguignon et al. 2016, 2017, Wang et al. 2019, Romero Arias et al. 2021, Bucek et al. 2021, *unpublished*), only a handful of species of Stotermitidae, Hodotermitidae, and Archotermopsidae have been included in termite phylogenetic trees. Because of this inadequate sampling, the historical biogeography of early-diverging termite lineages remains unclear. In this paper, we carried out a representative sampling of species belonging to Stotermitidae, Hodotermitidae, and Archotermopsidae. We obtained the nuclear ribosomal RNA genes (5S, 5.8S, 18S, 28S) and mitochondrial genomes of 27 samples collected across the distribution range of the group. We used this dataset to reconstruct time-calibrated phylogenetic trees and shed light on the historical biogeography of early-diverging termite lineages.

## 2.2 Materials and Methods

### 2.2.1 Sampling and sequencing

We sequenced eight samples of Stotermitidae, eight samples of Archotermopsidae, and seven samples of Hodotermitidae. In addition to these 23 samples, we also sequenced 36 termite species belonging to other families that we used as outgroups, including 17 species of Termitidae, 11 species of Rhinotermitidae, seven species of Kalotermitidae, and the only species of Mastotermitidae, *Mastotermes darwiniensis*. We combined these sequences with previously published mitochondrial genomes of one species of Stotermitidae, two species of Archotermopsidae, one species of Hodotermitidae, the only mastotermitid species *Mastotermes darwiniensis*, and one species of Cryptocercidae. Our final dataset comprised sequence data for 64 termite species and one non-termite cockroach species, *Cryptocercus punctulatus* (Table 2.1, Table S2.1).

Whole genomic DNA was extracted with the DNeasy Blood & Tissue kit using complete individuals, including guts. The concentration of DNA was measured with Qubit 3.0 fluorometer and adjusted to a concentration of 0.5 ng/μl. The Library of each sample was prepared separately with the NEBNext® Ultra™ II FS DNA Library Preparation Kit and the Unique Dual Indexing kit (New England Biolabs). Some samples were collected recently for genomic analyzes and were preserved in RNA-later® at -20°C or -80°C until DNA extraction. For these samples, we followed the manufacturer's protocol for library preparation, except for reagent volumes, which were reduced to one-fifteenth of the volumes advised by the manufacturer. We also used many samples collected over the past decades in alcohol and stored at room temperature for taxonomic purposes. The DNA of these samples was typically highly fragmented, and we, therefore, skipped the enzymatic fragmentation step during library preparation. We also reduced the volumes of all reagents to one-fifteenth of that suggested in the manufacturer's protocol. Other steps were performed as indicated in

the manufacturer's protocol. Libraries were pooled together and paired-end sequenced with the Illumina sequencing platform at a read length of 150 bp.

### **2.2.2 Assembly and Alignment**

We checked read quality using Fastp v0.20.1 (Chen et al. 2018). Read adapters and poly-G tails at the end of the reads were trimmed. Mitochondrial genome assembly and annotation were performed using MitoFinder v1.4 (Allio et al. 2020). Nuclear ribosomal RNA genes (5S, 5.8S, 18S, and 28S) were predicted using Barrnap v0.9 (Seemann 2013) from assemblies obtained with metaSPAdes v3.13.0 (Nurk et al. 2017). All genes were aligned separately using Mafft v7.305 (Kato 2002). For the 13 mitochondrial protein-coding genes, we carried out sequence alignment on the amino acid sequences translated using the transeq command of the EMBOSS suite of programs (Rice et al. 2000). Amino acid sequence alignments were converted into DNA sequence alignments using PAL2NAL v.14 (Suyama et al. 2006). The 22 mitochondrial transfer RNA genes and the six ribosomal RNA genes (mitochondrial 12S and 16S and nuclear 5S, 5.8S, 18S, and 28S) were aligned as DNA sequences. Individual gene alignments were concatenated using FASconCAT-G (Kück and Longo 2014).

### **2.2.3 Phylogenetic analyses**

All phylogenetic analyses were performed with and without the third codon positions of protein-coding genes. We reconstructed Maximum Likelihood phylogenetic trees using IQ-TREE 1.6.12 (Minh et al. 2020). The best-fit nucleotide substitution model was determined with ModelFinder implemented in IQ-TREE 1.6.12. Branch supports were calculated using 1000 bootstrap replicates. Bayesian phylogenetic trees were inferred with MrBayes v3.2.3 using the GTR+G model of nucleotide substitution (Ronquist et al. 2012). The Markov chain Monte Carlo (MCMC) chains were run for 30 million and 20 million generations for the datasets with or without the third codon positions of protein-coding genes, respectively. In all analyses, the MCMC chains were sampled every 5000 generations to estimate the posterior distribution. The first 10% of sampled trees were excluded as burn-in. Visual inspection of the trace files with Tracer v1.7.1 confirmed that all analyses converged (Rambaut et al. 2018). The effective sample size was higher than 220 for every parameter of every run. The MCMC chains were run four times in parallel for both datasets.

### **2.2.4 Divergence time estimation**

We reconstructed Bayesian time-calibrated phylogenetic trees using BEAST v2.6.2 (Bouckaert et al. 2019). Bayesian analyses were performed with and without the third codon positions of protein-coding genes. We used an uncorrelated lognormal relaxed clock to model rate variation among branches. A Yule model was used as tree prior. A GTR+G model of nucleotide substitution was applied to each partition. The MCMC analyses were run for 800 million generations and sampled every 5000 generations. We checked the convergence of the MCMC runs with Tracer v1.7.1 and consequently discarded the first 40% of generations as burn-in. We used ten fossils as time constraints (Table S2.2). Each calibration was implemented as an exponential prior on node time. The use of these calibrations has been thoroughly justified previously (Bucek et al. 2019, 2021, *unpublished*). We used TreeAnnotator implemented in the BEAST2 suite of programs to generate a consensus tree. Tree topology and 95% height posterior density (HPD) were visualized with FigTree v 1.4.4 (Rambaut 2018).

## **2.3 Results**

### **2.3.1 Phylogenetic reconstructions**

The phylogenetic trees obtained using Maximum Likelihood and Bayesian analyses received high nodal support values and possessed almost identical topologies. One exception was the

relationships among *Stolotermes inopinus* and the two samples of *Stolotermes ruficeps* that were resolved with low Bootstrap values (<75%) and Bayesian posterior probabilities (<0.9) (Figure 2.1).

Stolotermitidae was found to be monophyletic and formed the sister group of Archotermopsidae + Hodotermitidae. The Archotermopsidae were retrieved as paraphyletic in respect to the monophyletic Hodotermitidae. Within the lineage composed of Archotermopsidae and Hodotermitidae, *Hodotermopsis* was sister to the other five genera. *Zootermopsis* and *Archotermopsis* formed a monophyletic group sister to the three genera of Hodotermitidae. Within the Hodotermitidae, *Anacanthotermes* was found to be sister to *Hodotermes* + *Microhodotermes*. The eight genera from the three families were monophyletic.

### **2.3.2 Divergence dating**

Time-calibrated phylogenetic trees reconstructed with and without the third codon positions of protein-coding genes yielded similar time estimates, diverging by less than three million years. For this reason, we only provide the results of the analysis with the third codon position excluded (Figure 2.1). The clade composed of Stolotermitidae, Hodotermitidae, and Archotermopsidae diverged from other Euisoptera 123.3 Ma (112.9-135.8 Ma, 95% HPD). Stolotermitidae diverged from Hodotermitidae + Archotermopsidae 100.0 Ma (94.3-109.6 Ma, 95% HPD). The most recent common ancestor of Stolotermitidae roamed around 68.5 Ma (55.0-82.1 Ma, 95% HPD), and the most recent common ancestors of *Porotermes* and *Stolotermes* were estimated to live 20.2 Ma (15.5-25.2 Ma, 95% HPD) and 26.6 Ma (18.5-36.0 Ma, 95% HPD), respectively. *Hodotermopsis* and other Archotermopsidae + Hodotermitidae diverged 93.1 Ma (85.0-103.8 Ma, 95% HPD). The divergence time of *Zootermopsis* and *Archotermopsis* was estimated to have occurred 50.5 Ma (40.1-61.2 Ma, 95% HPD), and the most recent common ancestor of *Zootermopsis* was estimated at 19.8 Ma (15.0-25.1 Ma, 95% HPD). Hodotermitidae diverged from *Zootermopsis* + *Archotermopsis* 85.0 Ma (76.0-95.8 Ma, 95% HPD). Within the Hodotermitidae, *Hodotermes* + *Microhodotermes* diverged from *Anacanthotermes* 32.1 Ma (24.8-39.9 Ma, 95% HPD). *Hodotermes* and *Microhodotermes* split up 18.9 Ma (13.3-24.8 Ma, 95% HPD).

### **2.4 Discussion**

In this study, we present the most comprehensive phylogenetic reconstruction of the early-diverging termite families Stolotermitidae, Archotermopsidae, and Hodotermitidae. We used three phylogenetic reconstruction methods and repeated the analyses on datasets with and without third codon positions of protein-coding genes. The topology of the phylogenetic trees was largely consistent across methods and datasets, except for the positions of *Stolotermes inopinus* and *Stolotermes ruficeps*, which were discordant among analyses, probably owing to the limited amount of sequence data available for these two species. Our phylogenetic trees were also congruent with previous phylogenetic trees based on mitochondrial genomes and transcriptomes (Cameron et al. 2012, Bourguignon et al. 2015, Bucek et al. 2019). *Mastotermes* was found to be the sister group of Euisoptera, a clade including all termites but *Mastotermes* (Engel et al. 2009), and the group Stolotermitidae + Archotermopsidae + Hodotermitidae was sister to Neoisoptera + Kalotermitidae. Our analyses supported the monophyly of Stolotermitidae, which was found to be sister to the paraphyletic Archotermopsidae and its inner group, the monophyletic Hodotermitidae. The paraphyly of Archotermopsidae was already known from previous phylogenetic trees inferred from mitochondrial genome data (Bourguignon et al. 2015). Although the paraphyly of Archotermopsidae is strongly supported, in our views, it is premature to synonymize Archotermopsidae with Hodotermitidae, and the sequencing of additional nuclear markers is required before proceeding to nomenclatural changes.

The time-calibrated trees estimated with and without third codon positions of protein-coding genes yielded similar time estimates. Our time estimates of the branching among early-diverging termite families were younger than that of previous studies. However, our estimates were largely congruent with overlapping HPD intervals. For example, we estimated the most recent common ancestor of termites lived 133.2 Ma (125.5-145.6 Ma, 95% HPD), while previous studies found older ages: 149 Ma (136-170 Ma, 95% HPD) (Bourguignon et al. 2015), 151.3 Ma (149.3-153.7 Ma, 95% HPD) (Legendre et al. 2015), and 140.6 Ma (112.6-170.5 Ma, 95% HPD) (Bucek et al. 2019). Differences among studies in terms of fossil calibrations, fossil age estimations, taxonomic sampling, and models used for the reconstruction of time-calibrated trees may be the causes of these differences.

We did not attempt to reconstruct the ancestral range of Stolotermitidae + Archotermopsidae + Hodotermitidae. Ancestral range reconstructions have been performed previously for Neoisoptera and Kalotermitidae (Bourguignon et al. 2016, 2017, Wang et al. 2019, Romero Arias et al. 2021, Bucek et al. 2021). However, compared to Stolotermitidae + Archotermopsidae + Hodotermitidae, Neoisoptera and Kalotermitidae are diverse and widespread, comprising many extant species whose distribution and phylogenetic relationships can inform on past vicariance and dispersal events. Stolotermitidae, Archotermopsidae, and Hodotermitidae are species-poor families, with limited modern distributions, relictual of past wider distributions, as evidenced from the fossil record (Engel et al. 2013). Most geographic lineages of Stolotermitidae + Archotermopsidae + Hodotermitidae inhabit regions hosting no other members of the group, preventing a meaningful reconstruction of its historical biogeography.

While the low diversity of Stolotermitidae, Archotermopsidae, and Hodotermitidae hampered meaningful ancestral range reconstructions, our time-calibrated trees allowed to identify the origin of several biogeographic disjunctions. The two modern Stolotermitidae genera, *Porotermes* and *Stolotermes*, have a Gondwanan distribution (Krishna et al. 2013). However, our time-calibrated phylogenetic trees indicated that all species of *Porotermes* share a common ancestor 20.2 Ma (15.5-25.2 Ma, 95% HPD) and the common ancestor of the species of *Stolotermes* sequenced in this study lived 26.6 Ma (18.5-36.0 Ma, 95% HPD), after the breakup of Gondwana. Although we did not sequence *Stolotermes africanus*, the only species of *Stolotermes* found on the African continent, our time-calibrated trees showed that *Stolotermes* diverged from *Porotermes* 68.5 Ma (55.0-82.2 Ma, 95% HPD), after the breakup of Gondwana. These results imply that the presence of *Stolotermes* in South Africa, eastern Australia as well as New Zealand, and the presence of *Porotermes* in southern Australia, southern Africa, and South America is not the result of vicariance during the breakup of Gondwana, as discussed in previous studies (Krishna et al. 2013, Bourguignon et al. 2015). Instead, *Porotermes* and *Stolotermes* acquired their modern distribution through long-distance over-water dispersal events.

The biogeographic disjunctions among modern genera of Archotermopsidae + Hodotermitidae may be explained by land bridges. Indeed, we estimated that Archotermopsidae + Hodotermitidae shared a common ancestor that lived 93.1 Ma (85.0-103.8 Ma, 95% HPD), indicating vicariance through continental drift may explain the distribution of early-diverging Archotermopsidae. The Palearctic region remained connected to North America through Greenland until about 50 Ma (Scotese 2004), possibly explaining the disjunction between the Palearctic *Archotermopsis* and the Nearctic *Zootermopsis*, the modern descendants of more widespread ancestors (Krishna et al. 2013). The African *Hodotermes* + *Microhodotermes* diverged from *Anacanthotermes*, a genus found in Africa, the Middle East, and South Asia, 32.1 Ma (24.8-39.9 Ma, 95% HPD) and the most recent common ancestors of *Hodotermes* + *Microhodotermes* and *Anacanthotermes* lived 18.9 Ma

(13.3-24.8 Ma, 95% HPD) and 10.7 Ma (7.3-14.3 Ma, 95% HPD), respectively. The timing of the biogeographic disjunction between these two lineages may coincide with the existence of the *Gomphotherium* land bridge that connected Africa and Eurasia ~18-20 Ma (Rögl 1998, 1999). The sequencing of African *Anacanthotermes* in future studies is needed to confirm this scenario.

Our study showcases the importance of samples collected before the genomics era for future phylogenetic reconstructions. One limitation of many studies attempting to reconstruct the evolution of diverse taxa is the sampling of a representative set of specimens covering the diversity of the groups of interest. Because species of Stolotermitidae, Hodotermopsidae, Archotermopsidae, and Hodotermitidae occur in regions where termite diversity is generally low, we made fewer attempts to collect them. Instead, this study is largely based on samples collected in ethanol during the last three decades for taxonomic purposes. In addition, we sequenced a syntype of *Archotermopsis wroughtoni* (Desneux, 1904), that was collected in the Kashmir Valley. The systematic sequencing of type material, such as a syntype of *A. wroughtoni* sequenced in this study, holds the promise of clarifying the taxonomic literature and making available type-based species identification to the whole scientific community.

## 2.5 Conclusion

Termites are social cockroaches distributed worldwide. The ancestor of modern termites roamed around the Earth during the Early Cretaceous, some 140 million years ago, suggesting that both vicariance through continental drift and dispersal may have shaped the distribution of early-diverging termite lineages. We reconstruct the historical biogeography of three early-diverging termite families, Stolotermitidae, Hodotermitidae, and Archotermopsidae, using the nuclear rRNA genes and mitochondrial genomes of 27 samples. Our analyses confirmed the monophyly of Stolotermitidae + Hodotermitidae + Archotermopsidae, with Stolotermitidae diverging from the paraphyletic Archotermopsidae and the monophyletic Hodotermitidae 100.0 Ma (94.3-109.6 Ma, 95% HPD). The Oriental *Archotermopsis* and the Nearctic *Zootermopsis* diverged 50.5 Ma (40.1-61.2 Ma, 95% HPD) before the land connection between the Palearctic region and North America ceased to exist. The African *Hodotermes* + *Microhodotermes* diverged from *Anacanthotermes*, a genus found in Africa and Asia, 32.1 Ma (24.8-39.9 Ma, 95% HPD) and the most recent common ancestors of *Anacanthotermes* lived 10.7 Ma (7.3-14.3 Ma, 95% HPD), suggesting that *Anacanthotermes* dispersed to Asia using the land bridge connecting Africa and Eurasia ~18-20 Ma. In contrast, the common ancestor of modern *Porotermes* and *Stolotermes* species lived 20.2 Ma (15.5-25.2 Ma, 95% HPD) and 26.6 Ma (18.5-36.0 Ma, 95% HPD), respectively, indicating that the presence of these genera in South America, Africa, and Australia involved over-water dispersals. Our results suggest that early-diverging termite lineages acquired their current distribution through a combination of over-water dispersals and dispersals across land bridges.

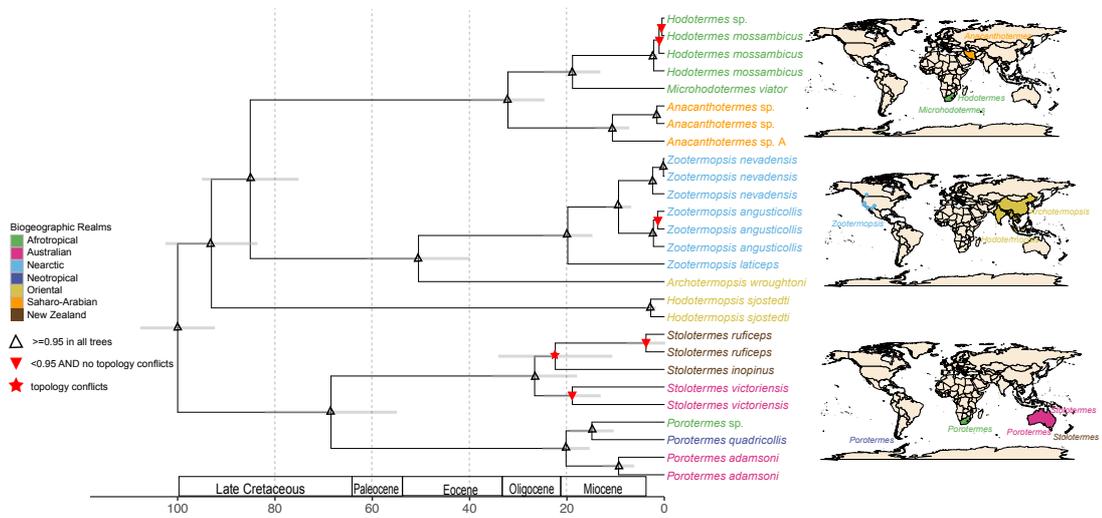


Figure 2. 1 Time-calibrated phylogenetic tree of Stolotermitidae, Archotermopsidae, and Hodotermitidae based on full mitochondrial genomes and 5S, 5.8S, 18S, and 28S rRNA genes.

The tree was reconstructed without third codon positions of protein-coding genes with BEAST2. The map shows the sampling locations of Stolotermitidae, Archotermopsidae, and Hodotermitidae. Node symbols (blank triangle, red triangle and red stars) represent the bootstrap support and posterior probability values obtained with IQTREE, MrBayes, and BEAST2 on the dataset with and without third codon positions of protein-coding genes. Node bars indicate 95% Height Posterior Density intervals of age estimates. Biogeographic realms are given and based on the descriptions in Holt et al. 2013. Tip colors coincide with collect localities. Maps on right show the collect localities of Hodotermitidae, Archotermopsidae and Stolotermitidae (from up to down).

Table 2.1 Sample comparisons among previous termite studies and this study

		No. of species recorded in Krishna et al. 2013	Legendre et al. 2008	Bourguignon et al. 2015	Bucek et al. 2019	In this study
MASTOTERMITIDAE	Mastotermitinae	1	1	1	1	1
ARCHOTERMOPSIDAE	<i>Archotermopsis</i>	2	1	0	0	1
	<i>Hodotermopsis</i>	1	1	1	1	1
	<i>Zootermopsis</i>	3	1	1	1	3
HODOTERMITIDAE	<i>Anacanthotermes</i>	16	0	0	0	2
	<i>Hodotermes</i>	2	1	0	0	2
	<i>Microhodotermes</i>	3	1	1	0	1
STOLOTERMITIDAE	Porotermitinae	3	1	1	1	3
	Stolotermitinae	7	1	0	0	3

## **Chapter 3 The origins of Malagasy termites (Blattodea: Termitoidae) driven by long-distance dispersal**

### **3.1 Introduction**

Madagascar is the world fourth largest island and is home to a great many endemic plant and animal species (Goodman and Benstead 2005, Buerki et al. 2013). One important reason for the peculiarity of its biota is its ancient isolation from other landmasses (Goodman and Benstead 2005). Madagascar, together with India, broke away from Africa ~160 million years ago (Ma) and has retained a distance of ~400 km from East Africa coast for the last 120 million years (Rabinowitz et al. 1983, Seward et al. 2004, Ali and Aitchison 2008, Seton et al. 2012). India subsequently broke away from Madagascar and started drifting northward, leaving Madagascar separated from other continental landmasses for the last ~88 Ma (Storey et al. 1995, Gnos et al. 1997). This long isolation is the source of Madagascar's unique biota.

The fauna of Madagascar has either been interpreted as resulting from vicariance or dispersal origin. Early biogeographers, unaware of the motion of continental landmasses, explained the origin of Madagascar fauna by long-distance over-water dispersals (e.g. Matthew 1915, Simpson 1940). Subsequently, the validation of the continental drift hypothesis (Wegener 1912) in the 1960s initiated a paradigm shift and vicariance became widely accepted as the dominant mechanism responsible for the Madagascar unique fauna (Noonan and Chippindale 2006, Bossuyt et al. 2006). However, the time-calibrated phylogenies produced during the last two decades have revealed that the majority of animal lineages found in Madagascar are younger than the split of Madagascar from continental Africa and India (e.g. Crottini et al. 2012). This timing implies that Madagascar predominantly acquired its fauna by means of long-distance over-water dispersals after its separation from other landmasses (Yoder and Nowak 2006, Ali and Vences 2019). For instance, the distributions of cichlids (Friedman et al. 2013), the extinct elephant bird (Mitchell et al. 2014), and the iconic chameleons (Raxworthy et al. 2002, Tolley et al. 2013) are all explained by such dispersals. Long-distance over-water dispersals also explain the distribution of several Malagasy insect lineages, such as the millipede assassin bugs (Forthman and Weirauch 2016), the beetle tribe Scarabaeini (Sole et al. 2011), and the hissing cockroaches (Bourguignon et al. 2018). Only a few insect lineages, such as the Malagasy alderfly genus *Haplosialis* (Liu et al. 2015), the cascade beetles (Toussaint et al. 2016) and the whirligig beetles (Gustafson et al. 2017) are ancient enough to have their modern distribution potentially resulting from vicariance.

Termites are a group of social cockroaches feeding on lignocellulose at various stage of decomposition, from hard wood to the organic matter present in the soil (Donovan et al. 2000, Bourguignon et al. 2011). They include ~3000 described species mostly distributed across the tropical and subtropical regions (Eggleton 2000a, Krishna et al. 2013). The oldest known fossils of termites are ~130 million years old (Myo) and date back from the early Cretaceous (Thorne et al. 2000a, Engel et al. 2016). Time-calibrated phylogenies provide slightly older age estimates and suggest that the last common ancestor of modern termites roamed the Earth 140-150 Ma (Engel et al. 2009, 2016, Legendre et al. 2015, Bourguignon et al. 2015, Bucek et al. 2019). The origin of termites therefore predates the breakup of Gondwana, indicating vicariance may explain the current distribution of early-diverging termite lineages. However, the termite fauna of Madagascar is known to comprise derived genera of Kalotermitidae and Neoisoptera (Sjöstedt 1926, Cachan 1949, 1951, Emerson 1960, Paulian 1970, Eggleton and Davies 2003, Monaghan et al. 2009) and appears to lack early-diverging termite lineages, such as Stolotermitidae and Archotermopsidae, whose

distribution may bear the signature of vicariance. Madagascar therefore acquired its modern termite fauna by means of long-distance over-water dispersals, presumably via rafting in floating wood pieces or vegetative rafts that contained parts of termite colonies (Gathorne-Hardy and Jones 2000, Thiel and Haye 2006).

The pathways and timing of the spread of termites across continents has been studied in details in Neoisoptera (Bourguignon et al. 2016, 2017, Wang et al. 2019, Romero Arias et al. 2021). However, the historical biogeography of Neoisoptera in Madagascar has been largely overlooked. Neoisoptera is composed of four families, Stylotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae, and contains upwards of 80% of described termite species (Engel et al. 2009, Krishna et al. 2013). The Neoisoptera are represented in Madagascar by a handful of endemic genera and by a few genera also found in continental Africa and in the Oriental region (Sjöstedt 1926, Cachan 1949, 1951, Emerson 1960). The only Malagasy termite lineage whose historical biogeography has been studied in details is the fungus-growing termite genus *Microtermes*, which colonized Madagascar from continental Africa via a single long-distance over-water dispersal ~13 Ma (Aanen and Eggleton 2005, Nobre et al. 2010). This dispersal event was presumably facilitated by the acquisition of a vertical mode of transmission of *Termitomyces* fungal symbionts in *Microtermes* (Nobre et al. 2010). The timing and geographic origin of other dispersal events, so well as the number of these dispersal events, are presently unknown and require further investigations.

In this study, we reconstructed robust time-calibrated phylogenetic trees of termites using the mitochondrial genomes of 586 Neoisoptera (including 93 Madagascan samples) and 14 outgroups. Our dataset is representative of the worldwide distribution of Neoisoptera and includes species from the Afrotropical, Australian, Madagascan, Nearctic, Neotropical (including Panamanian), Oriental (including Sino-Japanese), Palaearctic, Saharo-Arabian, and Oceanian realms, as defined by Holt et al. (2013). We used our time-calibrated phylogenetic trees to shed light on the evolution of Neoisoptera, the main termite lineage found in the Madagascan realm. Our specific aims were (i) to provide the first comprehensive phylogenetic tree of Malagasy Neoisoptera; and (ii) to investigate the geographic origin and the timing of dispersal and diversification of the Neoisoptera lineages present in Madagascar.

## **3.2 Material and Methods**

### ***3.2.1 Biological Samples and Mitochondrial Genome Sequencing***

We sequenced the mitochondrial genomes of 92 termite samples from Madagascar. We also sequenced an additional 30 mitochondrial genomes from termite samples collected outside Madagascar, including 13 samples from the Afrotropical realm, two samples from the Saharo-Arabian realm, nine Neotropical samples, one Oceanian sample and five Nearctic samples (Table S3.1). The mitochondrial genomes of these 30 samples were sequenced because they belonged to termite lineages underrepresented in previous studies. Most of these samples also belonged to termite lineages present in Madagascar, including *Amitermes*, *Psammotermes*, and *Prorhinotermes*. Their inclusion improves our reconstructions of ancestral ranges globally and for the Madagascan realm. We combined the 122 mitochondrial genomes sequenced in this study with 478 termite mitochondrial genomes previously published and available on GenBank, including the mitochondrial genome of the Madagascan *Prorhinotermes canalifrons* from Reunion Island (Cameron and Whiting 2007, Tokuda et al. 2011, Cameron et al. 2012, Bourguignon et al. 2015, 2016, 2017, Wang et al. 2019). We also obtained the mitochondrial genome of the cockroach *Cryptocercus relictus* (Cameron et al. 2012), a representative of Cryptocercidae, the sister group of termites. Specimens were tentatively identified based on available taxonomic works and similarity to

publicly available cytochrome oxidase subunit 2 (COII) sequences (Cachan 1949, 1951, Sands 1992, Inward et al. 2007b, Monaghan et al. 2009, Krishna et al. 2013).

We extracted DNA from two or three individuals preserved in RNA-later® or in 80% ethanol. Samples preserved in RNA-later® were stored at -20°C or -80°C until DNA extraction. Samples preserved in 80% ethanol were stored at room temperature for upwards of 20 years. We used one of the following three sequencing strategies: (i) long-range PCR followed by high-throughput DNA sequencing for samples stored in RNA-later®; (ii) whole-genome shotgun sequencing for samples stored in RNA-later®; and (iii) whole-genome shotgun sequencing for samples stored in 80% ethanol. In all three cases, DNA was extracted with the DNeasy Blood & Tissue extraction kit (Qiagen); and libraries were prepared using the NEBNext® Ultra™ II FS DNA Library Preparation Kit (New England Biolabs) and the Unique Dual Indexing Kit (New England Biolabs). Libraries preparation followed the manufacturer protocol for library preparation, except for reagent volumes, which were reduced to one-fifteenth of the recommended volumes.

For the (i) first strategy, DNA was extracted using specimens from which the digestive tract was removed. The whole mitochondrial genomes were amplified in two long-range PCR reactions using the TaKaRa LA Taq polymerase. We used the primer sets and PCR conditions previously described in Bourguignon et al. (2016). The concentration of the two long-range PCR products was measured with Qubit 3.0 fluorometer and both amplicons were mixed in equimolar concentration. One library was prepared for each sample separately, and libraries were pooled in equimolar concentration and paired-end sequenced using the Illumina Miseq2000 platform. For the (ii) second strategy, whole genomic DNA was extracted from whole body of termite workers including guts. Libraries were pooled in equimolar concentration and paired-end sequenced using the Illumina Hiseq2500 or Hiseq4000 platforms. For the (iii) third strategy, whole genomic DNA was extracted from whole body of termite workers including gut. Libraries were prepared without enzymatic fragmentation step because the DNA extracted from samples stored in 80% ethanol for a long period of time was highly fragmented. Libraries were pooled in equimolar concentration and paired-end sequenced using the Illumina HiSeq X or Novaseq platforms.

### **3.2.2 Assembly and Alignment**

Raw reads were quality-checked with Fastp v0.20.1 (Chen et al. 2018). Read adaptors were trimmed. Filtered reads were assembled using metaSPAdes v3.13.0 (Nurk et al. 2017), and retrieved and annotated with MitoFinder v1.4 (Allio et al. 2020). IMRA (Kinjo et al. 2015) was used as an attempt to elongate mitochondrial genomes which were not assembled in one contig. The control regions were omitted because they present repetitive patterns that are difficult to assemble with short reads.

All genes were aligned separately. The 22 transfer RNA genes and the two ribosomal RNA genes were aligned as DNA sequences with MAFFT v7.305 (Katoh and Standley 2013). The 13 protein-coding genes were translated into amino acid sequences and aligned using EMBOSS v6.6.0 (Rice et al. 2000) and MAFFT. Amino acid sequence alignments were back-translated into DNA sequences using Pal2Nal (Suyama et al. 2006). The 37 gene alignments were concatenated with FASconCAT-G\_v1.04.pl (Kück and Longo 2014).

### **3.2.3 Phylogenetic Analyses**

The concatenated sequence alignment was partitioned into five subsets: one for the combined transfer RNA genes, one for the combined ribosomal RNA genes, and one for each codon position of the protein-coding genes. The phylogenetic analyses were performed twice, with and without third codon positions. Phylogenetic relationships were inferred using both maximum likelihood and Bayesian Inference methods. We used IQ-TREE v1.6.12

(Nguyen et al. 2015) to reconstruct maximum likelihood phylogenetic trees. The best-fit nucleotide substitution model was determined with the Bayesian Information Criterion using ModelFinder (Kalyaanamoorthy et al. 2017) implemented in IQ-TREE. Branch supports were estimated using 1000 bootstrap replicates (Hoang et al. 2018). Bayesian analyses were implemented in MrBayes v3.2.3 using a GTR+G model of nucleotide substitution (Ronquist et al. 2012). The tree and the posterior distribution of parameters were estimated from Markov Chain Monte Carlo samplings. Each analysis was run with four chains, three hot and one cold. Each analysis was run in four replicates to ensure the convergence of the chains. For the analyses with third codon positions included, the chains were run for 40 million generations with 25% burn-in fraction. For the analyses without third codon positions, the chains were run for 20 million generations with burn-in fraction set to 10%. All the chains were sampled every 5,000 generations. The mixing of the chains and the behavior of all parameters were examined in Tracer v1.7.1 (Rambaut et al. 2018). For all analyses, the topology was constrained to harbor a sister relationship between the subfamilies Sphaerotermitinae and Macrotermitinae, as it was unambiguously evidenced in transcriptome-based phylogenies (Bucek et al., 2019).

#### **3.2.4 Divergence time estimation**

We analyzed the concatenated sequence alignments with and without third codon positions and reconstructed time-calibrated phylogenetic trees using BEAST v2.6.2 (Bouckaert et al. 2019, Zhang and Drummond 2020). Each analysis was run twice to ensure the convergence of the chain. The rate variation across branches was modelled using an uncorrelated lognormal relaxed clock. We used the Yule model for the tree prior. A GTR+G model of nucleotide substitution was assigned to each partition. For the analyses without third codon positions, we sampled the tree and parameter values of the chain every 50,000 steps over a total of 350 million generations. The first 10% of generations were discarded as burn-in. For the analyses with third codon positions included, the chain was run over 600 million generations and the first 20% sampled trees were discarded. The mixing of the chains and the behavior of all parameters were examined with Tracer v1.7.1 (Rambaut et al. 2018).

The molecular clock was calibrated using 14 fossils as minimum age constraints (Table S3.2). We used the youngest possible age for each fossil as reported in the Fossilworks database (Alroy 2016) (last accessed on January 2021, 31<sup>st</sup>). We used the criteria described by Parham et al. (2012) to select fossils. For each fossil calibration, we also determined a soft maximum bound using the phylogenetic bracketing approach described by Ho and Phillips (2009). Each calibration was implemented as exponential priors on node time. We previously justified the use of every fossil calibration used in Bucek et al. (2019) (Table 3.2). We used TreeAnnotator implemented in the BEAST2 suite of programs to generate a maximum clade credibility consensus tree. The trees were visualized with FigTree v1.4.4 (Rambaut 2018).

#### **3.2.5 Biogeographic analyses**

We reconstructed the historical biogeography of Neoisoptera, including the lineages present in the Madagascan realm using the R package BioGeoBEARS (Matzke 2013). The Madagascan realm includes Madagascar and neighbouring islands: the Comoros, Mascarenes, and Seychelles. We used sampling locations to assign each tip to a biogeographic realm. A total of six phylogenetic reconstructions, estimated with IQ-TREE, MrBayes, and BEAST2 (with and without third codon positions), were subjected to ancestral range reconstructions with BioGeoBEARS. Each analysis involved reconstructions with one of the three following models: DEC model (Dispersal-Extinction-Cladogenesis), DIVALIKE model (Dispersal-Vicariance Analysis), and BAYAREALIKE model. In addition, we also run each model using the setting “+ j” to allow jump dispersals, which

correspond to speciation events following long-distance dispersals (Matzke 2014). The six models above were used for each tree. The best-fit model was determined for each phylogenetic reconstruction using AICc (Akaike Information Criterion with sample size corrected) and LnL (log of the likelihood of data given the model) values (Table 3.3).

### 3.3 Results

#### 3.3.1 Topology of the phylogenetic trees

We used a total of 601 termite mitochondrial genomes, including 93 mitochondrial genomes from Madagascan samples. We reconstructed six phylogenetic trees using alignments with and without third codon positions using the maximum likelihood framework implemented in IQ-TREE and Bayesian inference in MrBayes and BEAST 2. The six phylogenetic trees were largely congruent with respect to interfamilial and intergeneric relationships, with the exception of a few nodes with low posterior probabilities and bootstrap supports (Figures 3.1, S3.1-3.6).

Our six phylogenetic trees showed that the Neoisoptera were represented by species belonging to ten lineages of Rhinotermitidae and Termitidae in the Madagascan realm (Figures 3.1, S3.1-S3.6). The Rhinotermitidae were represented by three species: *Prorhinotermes canalifrons*, *Coptotermes truncatus* and *Psammotermes voeltzkowi*. All three species belonged to genera also present in other biogeographic realms. The seven remaining lineages were part of the Termitidae and formed clades endemic to the Madagascan realm, including one clade of Macrotermitinae, two clades of Nasutitermitinae, and four clades of Termitinae. The only Madagascan clade of Macrotermitinae included several species of the genus *Microtermes* that were unambiguously retrieved as the sister group of a clade composed of African *Microtermes* and the Oriental *Ancistrotermes pakistanicus*. One of the two Madagascan clades of Nasutitermitinae contained *Malagasitermes milloti*, *Coarctotermes*, and several species assigned to the polyphyletic *Nasutitermes*. The sister group of this clade varied among analyses. The other Madagascan clade of Nasutitermitinae included only one species (*Nasutitermes* sp. 1), retrieved as sister to a group of Oriental species. The four Madagascan clades of Termitinae belonged to *Microcerotermes*, *Amitermes*, and the *Termes* group, which contained two Madagascan clades. The Madagascan clade of *Microcerotermes* was represented by upwards of nine species with an unresolved sister group. The genus *Amitermes* was represented by two species in the Madagascan realm and was retrieved as the sister group of a lineage including *Amitermes* species from the African, Saharo-Arabian, Oriental, and Australian realms. One of the two Madagascan clades of the *Termes* group was represented by two endemic Malagasy genera, *Quasitermes* and *Capritermes*, and their sister group, a species resembling *Quasitermes*. This first clade was itself retrieved as sister to a clade containing the Malagasy and Oriental species of *Termes* as well as the Australian members of the *Termes* group.

#### 3.3.2 Divergence times

The time-calibrated phylogenetic trees reconstructed with and without third codon positions of protein-coding genes diverged in their age estimates by up to 5 million years (Figures 3.1, S3.1 and S3.2). The age estimate divergences between analyses were smaller than 2.2 million years for the nodes representing the splits between Madagascan clades and their sister groups (Figures 3.1, S3.1 and S3.2). Given the similar divergence age estimates obtained with both types of analyses, we will only discuss the results of the analysis with third codon position excluded for the sake of simplicity.

All Madagascan clades of Neoisoptera diverged from their sister groups during the Miocene (Figure 3.2). Within the Rhinotermitidae, the Madagascan *Prorhinotermes*, *Psammotermes*, and *Coptotermes* diverged from their sister groups 9.0 Ma (95% height

posterior density (HPD): 6.0-12.1 Ma), 9.0 Ma (95% HPD: 5.0-13.2 Ma), and 8.4 Ma (95% HPD: 6.1-10.8 Ma), respectively. Within the Termitidae, the divergence between the Madagascan macrotermite *Microtermes* and their sister group was estimated at 16.6 Ma (95% HPD: 13.4-19.9 Ma). The divergence between the Madagascan nasutitermitine clade containing *Malagasitermes milloti* and *Coarctotermes* and its sister group was estimated at 14.4 Ma (95% HPD: 12.3-16.5 Ma). The divergence between the other Madagascan nasutitermitine clade, which contained *Nasutitermes* sp. 1, and its Oriental sister group was estimated at 10.7 Ma (95% HPD: 8.2-13.2 Ma). Within the termitines, we dated the divergence between Madagascan *Amitermes* and other *Amitermes* species at 13.1 Ma (95% HPD: 11.3-15.1 Ma). The most recent common ancestor of all Madagascan *Microcerotermes* and their sister group was estimated at 14.8 Ma (95% HPD: 12.5-17.2 Ma). The Madagascan *Quasitermes* + *Capritermes* clade was estimated to have diverged from its sister group 14.0 Ma (95% HPD: 11.6-16.5 Ma), while the Madagascan *Termes* sp. B diverged from its sister group 11.7 Ma (95% HPD: 9.5-13.9 Ma).

### 3.3.3 Biogeographic reconstruction

We used the six phylogenetic trees inferred in this study to reconstruct the ancestral range distribution of Neoisoptera using six different models implemented in BioGeoBEARS (*i.e.*, a total of 36 reconstructions). This strategy accounts for the uncertainties in phylogenetic reconstructions. The DEC + *j* model was the best-fit model for all trees, except for the BI trees with third position excluded for which the best-fit model was the DIVALIKE + *j* model (for details, see Table S3). Notably, the models with the parameter + *j* fit the data better than the models without this parameter, indicating that jump dispersals (or long-distance dispersals) played a major role in the biogeographic history of Neoisoptera.

Our analyses indicated that the Madagascan realm was colonized by seven to ten long-distance over-water dispersals (Figure 3.2). Four Neoisopteran lineages unambiguously colonized the Madagascan realm once: *Coptotermes truncatus* colonized the Madagascan realm from the Oriental realm; *Microtermes* from the Afrotropical realm; and *Microcerotermes* and *Amitermes* from an unidentified realm. The colonization of the Madagascan realm by *Prorhinotermes* + *Psammotermes*, the Nasutitermitinae, and the *Termes* group involved one or two long-distance over-water dispersals. Following the most likely scenario, *Prorhinotermes* and *Psammotermes* independently colonized the Madagascan realm through long-distance over-water dispersals from undetermined biogeographic realms. The alternative scenario of an early arrival of the common ancestor of *Prorhinotermes* and *Psammotermes*, followed by subsequent long-distance over-water dispersals to other biogeographic realms, was less likely but could not be excluded. Similarly, the two Madagascan clades of Nasutitermitinae probably originated from two independent dispersals from Africa to the Madagascan realm. A less likely alternative featured one long-distance over-water dispersal from Africa to the Madagascan realm followed by one dispersal to the Oriental realm. Lastly, the Madagascan realm was either colonized once by the *Termes* group followed by one or several dispersal events out of the Madagascan realm, or it was independently colonized twice, once by each Malagasy lineage of the *Termes* group.

## 3.4 Discussion

### 3.4.1 Long-distance over-water dispersals of Neoisoptera to and from the Madagascan realm: taxonomic identity, timing, and origin of the dispersers

We reconstructed the most comprehensive phylogenetic tree of Neoisoptera to date. The relationships among the main lineages of Neoisoptera were largely congruent with earlier molecular studies based on mitochondrial genome and transcriptome data (Bourguignon et al. 2015, 2017, Bucek et al. 2019). Our time estimates were generally younger than those found by these studies, but remained congruent, with overlapping HPD intervals. These

differences may pertain to the use of different fossil calibrations and/or to the changes of fossil age estimations at the time of publication of these studies. Although most of the fossils we used in this study and in previous studies were identical, some fossils were not used in all studies. For example, we previously used the ~110 Myo *Cratokalotermes santanensis* (Grimaldi et al. 2008) to calibrate Kalotermitidae + Neoisoptera (Bourguignon et al. 2015, 2017), while we now use the ~95 Myo *Archeorhinotermes rossi* (Krishna and Grimaldi 2003) to calibrate the same node. Another example is the ~95 Myo stoloitermitid fossil *Cosmotermes multus* (Zhao et al. 2019b), recently assigned to the new separate extinct family Arceotermitidae (Jiang et al. 2021), which we used for the first time in this study. This variation in the set of fossils used, combined with the age range estimations of fossil deposits that have been refined over the last ten years, may explain the variations among time estimates of different studies.

Before this study, three genera of Rhinotermitidae —*Coptotermes*, *Prorhinotermes* and *Psammotermes*— and four groups of Termitidae —*Microtermes*, *Microcerotermes*, the Nasutitermitinae and the *Termes* group— were known to be represented by species native to the Madagascan realm (Sjöstedt 1926, Cachan 1949, 1951, Emerson 1960, Eggleton and Davies 2003, Krishna et al. 2013). We sequenced upward of 40 Malagasy species, while Eggleton and Davies (2003) listed 33 species of Neoisoptera described from Madagascar, indicating the existence of several new species among our samples. Perhaps the most notable species were the two new species of *Amitermes*, a genus previously unknown from the Madagascan realm. We also found that the Malagasy species of Nasutitermitinae and of the *Termes* group do not form monophyletic groups. Therefore, the Madagascan termite fauna is more phylogenetically diverse than previously envisioned.

Our ancestral state reconstructions indicated that Neoisoptera colonized the Madagascan realm between seven to ten times independently and possibly dispersed out of the Madagascan realm up to four times. The dispersal events to and from the Madagascan realm took place 8.4-16.6 Ma (95% HPD: 6.1-19.9 Ma), between the mid-Miocene climatic optimum (Zachos et al. 2001) and the end of the Miocene. Therefore, our results indicate that the Madagascan realm acquired its fauna of Neoisoptera through long-distance over-water dispersal events.

In addition to dispersals to and from other biogeographic realms, our ancestral range reconstructions also revealed one long-distance over-water dispersal event within the Madagascan realm, that of *Prorhinotermes canalifrons* between Madagascar and the Reunion Island 2.1 Ma (95% HPD: 1.3-3.0 Ma). This species is also known from Mauritius, the Comoros, and the Seychelles (Krishna et al. 2013) potentially indicating additional over-water dispersals among islands of the Madagascan realm for this genus with high dispersal abilities and tolerance to salinity (Emerson 1955, Chiu et al. 2021). Two other species, *Coptotermes truncatus* and *Microcerotermes subtilis*, as well as the nasutitermitine genus *Kaudernitermes*, are also known from Madagascar and several neighboring islands (Krishna et al. 2013), indicating further dispersals between islands. Whether these dispersals were mediated by human activities or were long-distance over-water dispersals, as was the case for *P. canalifrons* in Madagascar and the Reunion islands, is unclear. Additional sequence data from the termite fauna of the Reunion Island, Mauritius, the Comoros, and the Seychelles are needed to identify the processes of colonization of these islands.

We were able to identify the source of three dispersal events to the Madagascan realm: *Coptotermes truncatus* has Oriental origin, the Malagasy *Microtermes* have African origin as previously shown by Aanen and Eggleton (2005), and the nasutitermitines arrived from Africa at least once. The origin of other Madagascan lineages remains unresolved. Therefore, our results do not provide a global picture of the origin of the Madagascan Neoisoptera,

although we show that some lineages have African and Oriental origins, as is the case for many other taxa (Yoder and Nowak 2006, Warren et al. 2010). Our ancestral range reconstructions also point to the possibility that Neoisoptera dispersed out of the Madagascan realm on multiple occasions, although these events remain speculative. Additional sequences from other biogeographical realms are required to identify the origin of Madagascan Neoisoptera lineages with yet unresolved origin.

### **3.4.2 The colonization of the Madagascan and Australian realms by Neoisoptera coincides with the global expansion of grasslands**

The colonization of the Madagascan realm by Neoisoptera coincides with the colonization of the Australian realm (Bourguignon et al. 2016, 2017, Arab et al. 2017, Wang et al. 2019) (Figure 3.2). The colonization of both realms was initiated around the Miocene climatic optimum, 15-17 Ma, and continued over the next five to ten million years while the world climate gradually cooled down (Zachos et al. 2001) and grasslands expanded worldwide (Edwards et al. 2010). It is therefore tempting to attribute this coincidental timing to shared historical climatic and ecological changes in Australia and Madagascar.

The climate of Australia became drier during the Middle Miocene ~14 Ma, and new biomes composed of flora and fauna adapted to arid conditions expanded (Martin 2006, Crisp and Cook 2013). The expansion of the arid-adapted biomes in Australia was accompanied by the opening of new ecological opportunities for local Australian taxa and for colonizers arriving from other continents (Crisp and Cook 2013), which included a dozen of lineages of Neoisoptera (Bourguignon et al. 2016, 2017, Arab et al. 2017, Wang et al. 2019, Clement et al. 2021). Unlike in Australia, the origin of grasslands in Madagascar is still debated. Human activities have undoubtedly contributed to the expansion of modern Madagascar's grasslands and some authors have argued that, prior to human arrival, the areas presently covered by grasslands were forested and only contained patches of grasslands (Joseph and Seymour 2020, Crowley et al. 2021). The alternative view is that Madagascar's grassland first appeared during the Miocene and gradually expanded, an expansion that was accelerated by human arrival (Bond et al. 2008, Vorontsova et al. 2015, Solofondranohatra et al. 2020, Salmona et al. 2020). Whichever scenario turns out to be correct, the arrival of Neoisoptera in the Madagascan realm was concurrent to the diversification of grasses in Madagascar, whose number of species exponentially increased since around 20 Ma (Hackel et al. 2018). The divergence between the two grass-feeding species *Coarctotermes pauliani* and *Coarctotermes baharaensis* 6.5 Ma (95% HPD: 4.2-8.8 Ma) indicates an early adaptation of some termite species to grassland in Madagascar. However, the bulk of the termite diversity in Madagascar is associated with forested areas (Eggleton and Davies 2003). The colonization of Madagascar and Australia by Neoisoptera therefore coincides with the global spread of grasses.

In addition to the timing of colonization, another parallel that can be made between the Neoisopteran fauna of the Madagascan and Australian realms is the similarity of their taxonomic composition. The Madagascan realm was colonized by two genera not found in Australia, the rhinotermitid *Psammotermes* and the termitid *Microtermes* (Cachan 1949), while the Australian realm was colonized by three genera absent from Madagascar, the rhinotermitids *Schedorhinotermes*, *Parrhinotermes* and *Heterotermes* (Hill 1942, Watson and Abbey 1993). Note that *Heterotermes philippinensis* was introduced in Madagascar and in Mauritius (Cachan 1950, Evans et al. 2013). In contrast, both realms were colonized by the rhinotermitid genera *Coptotermes* and *Prorhinotermes* and by the termitid genera *Microcerotermes*, *Amitermes*, *Termes* and *Nasutitermes* (Hill 1942, Cachan 1949, Watson and Abbey 1993). Of note, the latter three genera are paraphyletic and include a number of genera endemic to the Madagascan and Australian realms nested within them. Therefore,

these two realms host taxonomically similar communities of Neoisoptera, acquired within the same geological time interval. These observations suggest the existence of ecological preadaptations in the Neoisopteran lineages that colonized Madagascar and Australia, two distant landmasses presently dominated by grasslands and savannah biomes.

We previously reconstructed the global spread of Neoisoptera without samples from Madagascar (Bourguignon et al. 2016, 2017, Wang et al. 2019, Romero Arias et al. 2021). In this paper, we sequenced the mitochondrial genomes of 92 termite samples from Madagascar, which provide a key opportunity to refine the picture of the global spread of Neoisoptera. The higher termites, which make up over 80% of species of Neoisoptera (Krishna et al. 2013), originated from Africa and dispersed worldwide in two phases (Bourguignon et al. 2017). During the first phase, which spanned the Oligocene and the early Miocene, ~34-20 Ma, higher termites colonized the Neotropical and Oriental realms via a dozen of over-water dispersal events (Bourguignon et al. 2017). Our results show that the second phase, which took place during the Miocene, ~20-8 Ma, was characterized by the colonization of Australia and Madagascar by higher termites and coincides with the global expansion of grasslands.

### **3.5 Conclusion**

Madagascar is home to many endemic plant and animal species owing to its ancient isolation from other landmasses. This unique fauna includes several lineages of termites, a group of insects known for their key role in organic matter decomposition in many terrestrial ecosystems. How and when termites colonized Madagascar remains unknown. In this study, we used 601 mitochondrial genomes, 92 of which were generated from Malagasy samples, to infer the global historical biogeography of Neoisoptera, a lineage containing upwards of 80% of described termite species. Our results indicate that Neoisoptera colonized Madagascar between seven to ten times independently during the Miocene, between 8.4-16.6 Ma (95% HPD: 6.1-19.9 Ma). This timing matches that of the colonization of Australia by Neoisoptera. Furthermore, the taxonomic composition of the Neoisopteran fauna of Madagascar and Australia are strikingly similar, with Madagascar harboring an additional two lineages absent from Australia. Therefore, akin to Australia, Neoisoptera colonized Madagascar during the global expansion of grasslands, possibly helped by the ecological opportunities arising from their spread in this new biome.



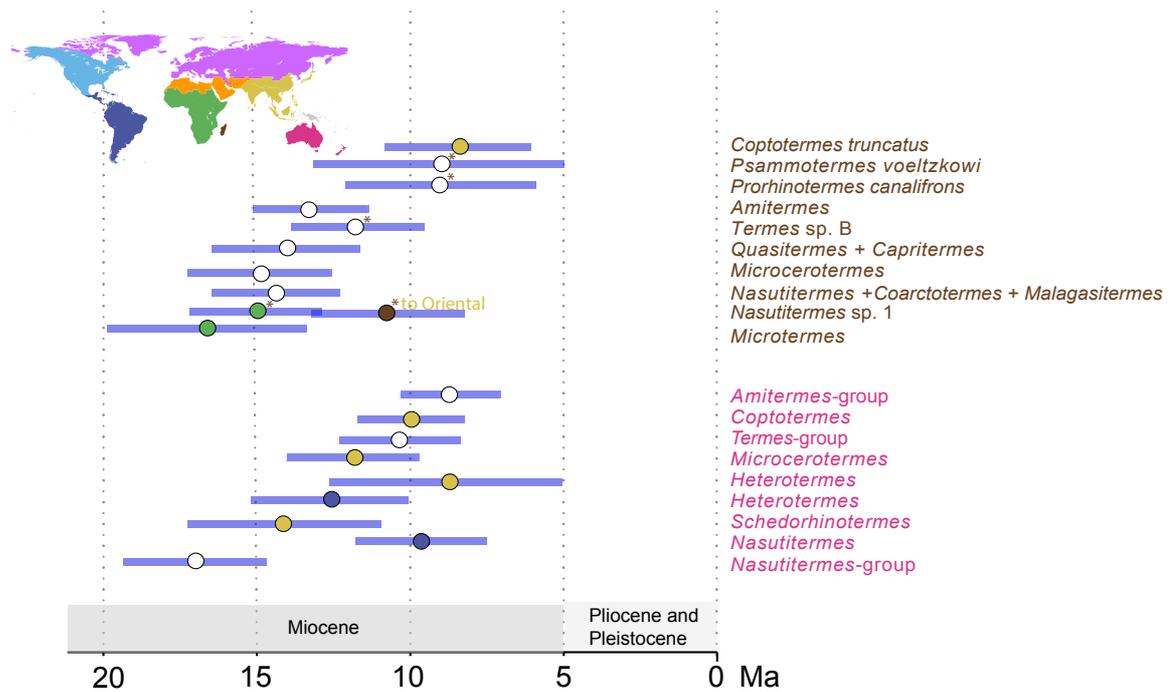


Figure 3. 2 Summary of Madagascar colonization and 'out-of-Madagascar' events.

Node bars indicate the 95% HPD intervals estimated with BEAST 2. The colors of node circles indicate ancestral ranges reconstructed with probabilities higher than 95% for the six phylogenetic trees inferred with IQ-TREE, MrBayes and BEAST 2, with and without third codon positions. White circles indicate undetermined ancestral distribution. The map shows the biogeographic realms recognized in this study (modified from Holt et al. 2013). Asterisks indicate the dispersal events that could not unambiguously be assigned with an origin and direction.

## **Chapter 4 The evolution and diversification of termites from America inferred from a near-complete phylogeny**

### **4.1 Introduction**

Adaptive radiations are lineages that experienced rapid species diversification, often in response of new ecological opportunities (Schluter 2001, Yoder et al. 2010, Glor 2010, Myers and Burbrink 2012). The importance of ecological opportunities on adaptive radiations was first recognized by Simpson (1953). Four factors can be at the origin of new ecological opportunities: 1) new available resources, 2) the colonization of new landmasses, 3) the extinction of competitors or predators, and 4) the acquisition of key innovations (Simpson 1953, Myers and Burbrink 2012). In many cases, the rise of adaptive radiations coincides with major global changes. For example, the extinction of non-avian dinosaurs following the collision of the Earth by an asteroid coincides with the rise to dominance of mammals (Meredith et al. 2011, Maor et al. 2017). In the case of termites, one past climatic event, the global cooling that was initiated at the Miocene-Oligocene boundary (Zachos et al. 2001), coincides with the rise of termites as the main decomposers in tropical and subtropical terrestrial ecosystems (Bourguignon et al. 2017).

Previous studies have shown termite origins date back to the Early Cretaceous, some 140 million years ago (Ma) (Bourguignon et al. 2015). However, vicariance through continental drift does not explain the current distribution of modern termites, including the distribution of early-diverging termite lineages (Wang et al. Chapter 2). Instead, long-distance dispersal events, either achieved via transoceanic rafting or land bridges, have been commonplace during termite evolution, explaining the distribution patterns of most termite lineages (Bourguignon et al. 2015, 2016, Wang et al. 2019, Romero Arias et al. 2021). Successful dispersers, colonizing new landmasses, have the opportunity to fill the ecological niches available, possibly escaping the pressure exerted by the predators and competitors present in their native range. Following arrival to their new destination, the first termite colonizers, possibly freed of inter-species competition, may have diversified and fill available niches quickly. Rapid bursts in diversification following successful colonization events of new geographical areas are commonly found across the tree of life (e.g (Condamine et al. 2020, Li et al. 2021)). The alternative scenario, that the first termite colonizers diversified gradually and steadily since their ancestor successfully colonized new geographic areas is also possible. A robust phylogeny including representative of most modern termite species has the potential to determine which of these two alternative scenarios is correct.

Termites consist of ~3000 described species, most of which inhabit tropical and subtropical terrestrial ecosystems (Eggleton 2000b, Krishna et al. 2013). South America, which we will refer to as the Neotropical realm, hosts the second most species-rich communities of termites in the world, harboring a total of 612 described species classified into 107 genera (Constantino 2016). The Neotropical region extends North to South from the lowlands of Mexico to Patagonia and includes the entire South American continent and the Caribbean islands (Sclater 1858, Constantino 2002). The region is diverse, covered by various types of ecosystems, including rainforests, savannas, caatingas, and open grasslands (Constantino 2008). Wood-feeding termites are found across the whole continent, while their humus-feeding and soil-feeding counterparts are mostly found in tropical rainforests (Eggleton 2000b, Constantino 2002, Jones and Eggleton 2011). Previous studies have shown that the higher termites colonized the world during the global cooling that was initiated at the Eocene-Oligocene boundary (Morley 2000, Bourguignon et al. 2015, 2017). The lineages of Neoisoptera native to the Neotropical region colonized the continent during the Oligocene and Miocene (Bourguignon et al. 2016, 2017, Wang et al. 2019). In contrast, the

Neotropical region form the cradle of modern Kalotermitidae (Bucek et al. Submitted). Many studies have focused on termites from the Neotropics with the aims of resolving their taxonomic and functional diversity (e.g. Davies et al. 2003, Palin et al. 2011, Nunes et al. 2017, Carrijo et al. 2020), yet, a complete phylogeny of the termites from that region is missing.

North America, which we will refer to as the Nearctic realm, is species-poor in comparison to the Neotropical realm, hosting 51 described species classified into 19 genera (Constantino 2016). The Nearctic realm extends from Greenland to central Mexico and is covered with semi-deserts, temperate woodlands, and temperate rain forests (Sclater 1858, Jones and Eggleton 2011). The diversity of termites in the Nearctic region has also been studied (e.g. Nelson et al. 2001, Hyseni and Garrick 2019, Blumenfeld and Vargo 2020), and like is the case for the Neotropical termite fauna, no complete phylogeny of Nearctic termites is available.

The processes behind the rise to dominance of termites remain largely unknown. We focused on the American termite fauna in order to determine how termites diversified and became the major decomposers of the tropics and subtropics. We sequenced over 2000 termite samples collected from the Nearctic and Neotropical realms over the last three decades. Our near-complete phylogeny will help to determine how termites diversified in this geographic region. Our study is a rare attempt to reconstruct a near-complete phylogeny for a group of arthropods across two continents.

## **4.2 Methodology**

### **4.2.1 Sample collection**

This project was carried out in collaboration with several overseas researchers who provided termite samples. We sequenced 1306 termite samples collected by Professor Rudolf Scheffrahn and his team, ~1000 termite samples collected by Professor Eliana Canello and her team, and about 100 samples collected by Professor Yves Roisin and Professor Bourguignon. These samples were collected across North and South America over the last 30 years. The samples have been selected in order to be representative of the diversity of termites in the Neotropical and Nearctic realms. Therefore, our sampling effort encompasses almost all described species from the new world and numerous species that are still awaiting formal description. A list of the samples can be provided if needed.

### **4.2.2 Molecular data collection**

In total, 2564 samples have been sequenced. Whole genomic DNA was extracted with the DNeasy Blood & Tissue extraction kit (Qiagen). Libraries were prepared using the NEBNext® Ultra™ II FS DNA Library Preparation Kit (New England Biolabs) and the Unique Dual Indexing Kit (New England Biolabs). Libraries were prepared with one of the following two strategies: (i) for samples collected in pure ethanol and stored in freezer, libraries were prepared following the manufacturer's library preparation protocol scaled down to 1:15; (ii) for samples collected 10-30 years ago, libraries were prepared without fragmentation step and scaled down to 1:15, while other steps were performed as per the manufacturer's protocol. Libraries were sequenced using the Illumina HiSeqX, Illumina HiSeq4000, or Novaseq 6000 platforms.

### **4.2.3 Phylogenetic analyses**

Raw reads were quality-checked and adapters were trimmed using Fastp v0.20.1 (Chen et al. 2018). Mitochondrial genomes were assembled with MetaSPAdes v3.13.0 (Nurk et al. 2017) and annotated with MitoFinder v1.4 (Allio et al. 2020). IMRA was used to join the contigs of mitochondrial genomes that were not originally assembled into one scaffold (Kinjo et al. 2015). The control region of mitochondrial genomes was discarded because this repeated region is difficult to assemble with short reads. Nuclear ribosomal RNA genes (5S, 5.8S, 18S, and 28S) were predicted using Barrnap v0.9 (Seemann 2013). Ultraconserved

elements (UCEs) were retrieved with the preliminary UCE Database designed for termites by Dr. Hellems (unpublished data) using PHYLUCE v1.6.6 (Faircloth et al. 2012, Faircloth 2016).

The sequences of each protein-coding gene were translated into amino acid sequences using EMBOSS v6.6.0 (Rice et al. 2000) and aligned separately with MAFFT v7.305 (Kato and Standley 2013). Amino acid sequence alignments were back-translated into DNA alignments with Pal2Nal (Suyama et al. 2006). The two mitochondrial ribosomal RNA genes (12S and 16S), the 22 transfer RNA genes and the UCEs were aligned as DNA sequences with MAFFT v7.305. All alignments were concatenated with FASconCAT-G\_v1.04.pl (Kück and Longo 2014).

The final concatenated alignment was analyzed as a whole dataset without partitioning. Phylogenetic relationships were reconstructed using the Maximum likelihood method implemented in IQ-TREE v1.6.12 (Nguyen et al. 2015). The best nucleotide substitution model was identified to be a GTR+F+R10 model by ModelFinder implemented in IQ-TREE (Kalyaanamoorthy et al. 2017). Branch supports were estimated using 1000 bootstrap replicates. The phylogeny was visualized and edited using FigTree v1.4.4 (Rambaut 2018).

#### **4.3 Preliminary Results**

We reconstructed a near complete phylogenetic tree of termites from America using the sequences of 2457 termite samples. The first preliminary tree is shown in Figure 4.1. This tree was first used to correct taxonomic misidentifications and sequencing error that may happen during wet lab work. Several mis-reconstructed phylogenetic relationships among species were detected after the tree visualization. It may result from misidentification, mislabeling, improper adaptor usage during library preparation or library pooling, and bioinformatical mistakes during molecular data analysis.

#### **4.4 Future plan**

We will generate a dataset curated for taxonomic identifications and sequence data. In order to identify every termite lineage having independently colonize America, we will include in our dataset the sequences of about 500 termite species collected from every other continent. All these sequences have been published in previous studies. The phylogenetic relationships among termite lineages from America will be reconstructed using the maximum likelihood method implemented in IQ-TREE v1.6.12 (Ronquist et al. 2012, Nguyen et al. 2015). Divergence time will be estimated for each phylogenetic tree using a set of 14 fossils and the program MCMCTree (Yang 2007). To investigate the diversification history of each termite clade, we will calculate the diversification rate using the Bayesian Inferences with implemented in the R package BAMMtools (Rabosky 2014). Lineage-through-time plots with diversification shifts (LTT-Plot) will also be calculated for each American termite clade separately (Rabosky 2006, 2014, Rabosky and Lovette 2008). These analyses will allow to determine how termites diversified in America.

Figure4. 1 A near complete phylogenetic tree of termites from America inferred from protein coding genes, nuclear ribosomal RNA and Ultraconserved elements of 2457 samples.



## Conclusion

In Chapter 1, I reconstructed the ancestral range of Rhinotermitinae, a group of Rhinotermitidae sister to Serritermitidae, Termitidae, and all other Rhinotermitidae. Using the time-calibrated phylogenetic trees inferred from the complete mitochondrial genomes of 27 samples of Rhinotermitinae, I reconstructed the historical biogeography of the group and found that all general of Rhinotermitinae are monophyletic. The Rhinotermitinae arose 50.4–64.6 Ma (41.7–74.5 Ma 95% HPD). The first split within the Rhinotermitinae is that of *Parrhinotermes* with *Dolichorhinotermes* + *Rhinotermes* + *Schedorhinotermes*, which was estimated at 29.7–42.4 Ma (23.3–50.0 Ma 95% HPD). *Dolichorhinotermes* + *Rhinotermes* diverged from *Schedorhinotermes* 24.0–35.7 Ma (16.8–45.3 Ma 95% HPD). Rhinotermitinae acquired their current distribution via combined transoceanic and land bridge dispersal events between Eocene and Miocene periods. Because of the large intervals of the age estimations and the uncertainties of ancestral range reconstructions we could not draw final conclusions on the dispersal events. Although the sequencing of more samples, for example of the Neotropical *Acorhinotermes* and the Oriental *Macrorhinotermes*, are needed to draw a more complete picture of the historical biogeography of Rhinotermitinae, our phylogenetic analyses revealed the role played by long-distance over-water dispersal on the global distribution of modern termites.

In Chapter 2, I resolved the historical biogeography of the three early-diverging termite families, Stolotermitidae, Hodotermitidae, and Archotermopsidae. The historical biogeography of early-diverging termite lineages has remained unclear because of inadequate sampling. I reconstructed time-calibrated phylogenies using the complete mitochondrial genomes and nuclear rRNA genes of 27 samples. My phylogenetic trees confirmed the monophyly of Stolotermitidae and the paraphyly of Archotermopsidae with respect to the monophyletic Hodotermitidae. The most recent common ancestor of Stolotermitidae + Hodotermitidae + Archotermopsidae was estimated at 100.0 Ma (94.3–109.6 Ma, 95% HPD). The Oriental *Archotermopsis* and the Nearctic *Zootermopsis* diverged 50.5 Ma (40.1–61.2 Ma, 95% HPD). The African *Hodotermes* + *Microhodotermes* diverged from the Saharo-Arabian *Anacanthotermes* 32.1 Ma (24.8–39.9 Ma, 95% HPD). The most recent common ancestors of *Anacanthotermes* was estimated at 10.7 Ma (7.3–14.3 Ma, 95% HPD), suggesting that the Saharo-Arabian *Anacanthotermes* arrived via the land bridge connecting Africa and Eurasia. The most recent common ancestor of modern *Porotermes* and *Stolotermes* species were dated at 20.2 Ma (15.5–25.2 Ma, 95% HPD) and 26.6 Ma (18.5–36.0 Ma, 95% HPD), respectively, indicating that these genera acquired their current distribution after several over-water dispersals. Overall, our time-calibrated phylogenetic trees show that early-diverging termite lineages dispersed to acquire their modern distribution, and that vicariance through continental drift played a minor role.

In Chapter 3, I reconstructed the global historical biogeography of Neoisoptera in Madagascar. The historical biogeography of Neoisoptera has been studied in details in the past few years; however, no samples from Madagascar have been included in these phylogenies. Given that Madagascar has been isolated from other continents for upward of 100 million years, the inclusion of Malagasy samples in the phylogenetic trees is crucial to improve our understanding of termite historical biogeography. Using the mitochondrial genomes of 93 termite samples collected in the Madagascan realm, I reconstructed robust phylogenetic trees of Neoisoptera in order to refine our understanding of the dispersal events that shaped the modern distribution of Neoisoptera. Using the time-calibrated tree inferred from 601 mitochondrial genomes and 14 fossil calibrations, I found the Neoisoptera

## Conclusion

colonized Madagascar between seven and ten times independently during the Miocene. Interestingly, the timing and the taxonomic composition of dispersers match that of Australia. These results suggest that the same factors, the global expansion of grasslands, favored the colonization of Madagascar and Australia by Neoisoptera. I also found several possible “out-of-Madagascar” events that occurred between the middle and the end of the Miocene. Thus, as is the case for the termite fauna of other biogeographic region, the Neoisoptera fauna of Madagascar arrived through multiple long-distance transoceanic dispersals.

In Chapter 4, I focused on the American termite species and reconstructed the most comprehensive phylogenetic tree of termites for this geographic region. I am presently unable to draw large conclusions about this work because of some misidentification, mislabeling, improper adaptor usage during library preparation, or library pooling, and bioinformatical mistakes that I will solve during the coming months. The American region host a diverse fauna of termites, consisting of around 670 described species living in the diverse American tropical ecosystems. My near-complete phylogenetic tree of termites, including over 2000 samples, will help to investigate the diversification history of termites in America. It also provided a valuable piece of work for the researchers working on the termites of the North and South American continents.

Overall, the results of my thesis largely filled the gaps that were left in our understanding of the historical biogeography of termites. Future studies should focus on reconstructing a complete phylogenetic tree of termites including all modern species. A complete phylogenetic tree of termites would be of interest for various reasons:

- (1) It would assist taxonomists in their revision of the termite nomenclature and help them to synonymize the many redundant names still present. It would also provide a platform to revise paraphyletic and polyphyletic taxa. This could be assisted by the sequencing of type material, as I did in this thesis with the sequencing of the syntype of *Archotermopsis wroughtoni*.
- (2) It would provide invaluable tools for every termite biologist, helping them to identify the taxonomic names of the species they are working on, thence facilitating comparisons among studies.
- (3) The sequences generated to build phylogenetic trees could also be used for other purposes, such as the establishment of a mitochondrial genome reference database that could be used to study environmental DNA. This database could speed up the assessment of termite communities in degraded and pristine environments.

My thesis represents one step forward toward this goal of generating a complete termite phylogeny.

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Appendices

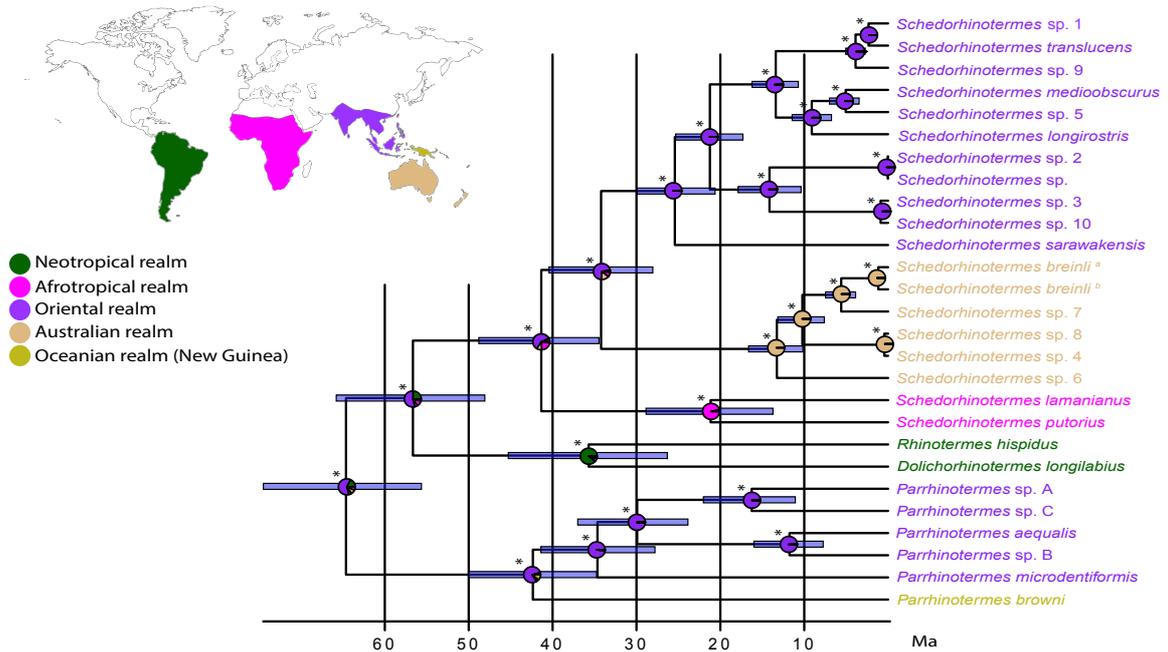


Figure S1. 1 Reconstruction of Rhinotermitinae ancestral distribution and estimates of cladogenesis time based on whole mitochondrial genome, including third codon positions.

The map shows the biogeographic areas that were described in Holt et al. 2013. Phylogenetic tree was estimated in BEAST v1.8.4. Branch support values indicate posterior probability. Asterisks indicate 1.0 posterior probability. The bars at the nodes indicate the 95% HPD intervals for the ages. Pie charts indicate likelihoods of ancestral geographic range reconstruction.

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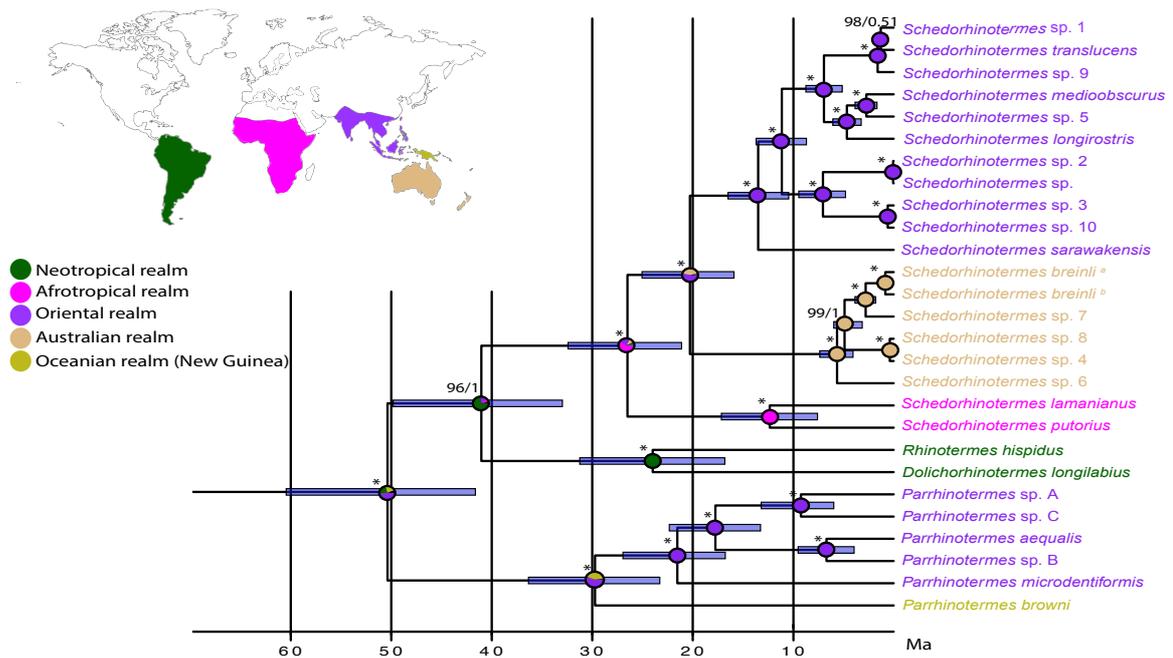


Figure S1. 2 Reconstruction of Rhinotermitinae ancestral distribution and estimates of cladogenesis time based on whole mitochondrial genome, with third codon positions excluded.

The map shows the biogeographic areas that were described in Holt et al. 2013. Phylogenetic tree was estimated in RAXML and MrBayes. Branch support values indicate maximum-likelihood bootstrap support (percentage) and posterior probability in RaxML and MrBayes trees, respectively. Asterisks indicate 100% bootstrap support and 1.0 posterior probability. The bars at the nodes indicate the 95% HPD intervals for the ages. Pie charts indicate likelihoods of ancestral geographic range reconstructed with a Bayesian binary model with estimated state frequencies and gamma-distributed rates across sites.

## Appendices

Table S1. 1 Rhinotermitinae samples used in this study, with details of collection locality, date of collection, sample code, collection holder, and GenBank accession numbers. Collection holders: JŠ, Jan Šobotník; YR, Yves Roisin.

Species	Collection Locality	Date	Sample code	Collection holder	Reference	GenBank Accession Number
<i>Dolichorhinotermes longilabius</i>	Petit Saut, French Guiana	01-Feb-11	NA	JŠ	Bourguignon et al. 2015	
<i>Parrhinotermes aequalis</i>	near Kuala Belait, Brunei	13-Feb	TBRU1.1b	JŠ		MK246849
<i>Parrhinotermes browni</i>	50 km from Nabire, West Papua, Indonesia	01-Jun-11	NG52	JŠ	Bourguignon et al. 2015	
<i>Parrhinotermes microdentiformis</i>	near Kuala Belait, Brunei	13-Feb	TBRU1.22c	JŠ		MK246851
<i>Parrhinotermes</i> sp. C	Penang, Malaysia	13-Jul	MAL29	JŠ		MK246842
<i>Parrhinotermes</i> sp. A	Khao Chong, Thailand	03-Nov-13	THAI023	JŠ		MK246854
<i>Parrhinotermes</i> sp. B	Bukit Batog, Singapore	13-Dec	T6.9a	JŠ		MK246848
<i>Rhinotermes hispidus</i>	Petit Saut, French Guiana	14-Oct	G751	YR	Bourguignon et al. 2016	
<i>Schedorhinotermes breinl<sup>a</sup></i>	19 km. Nth of Ayr, QLD, Australia	08-May-08	ISO314		Cameron et al. 2012	
<i>Schedorhinotermes breinl<sup>b</sup></i>	near Gordonvale, Queensland, Australia	13-Feb-13	AUS87	JŠ		MK246841
<i>Schedorhinotermes lamanianus</i>	Yangambi, D.R. Congo	12-Jul-13	RDCT112	YR		MK246844
<i>Schedorhinotermes longirostris</i>	Mac Ritchie, Singapore	12-Dec	T2.13c	JŠ		MK246846
<i>Schedorhinotermes medioobscurus</i>	Mac Ritchie, Singapore	13-Dec-12	SING75	JŠ		MK246845
<i>Schedorhinotermes putorius</i>	Yangambi, D.R. Congo	05-Jul-13	RDCT003	YR		MK246843
<i>Schedorhinotermes sarawakensis</i>	near Kuala Belait, Brunei	13-Feb	TBRU2.3A	JŠ		MK246852
<i>Schedorhinotermes</i> sp.	near Nan, Thailand	12-Nov-13	THAI084	JŠ		MK246857
<i>Schedorhinotermes</i> sp. 1	Khao Chong, Thailand	03-Nov-13	THAI030	JŠ		MK246855
<i>Schedorhinotermes</i> sp. 2	Thung Chang, Thailand	13-Nov-13	THAI092	JŠ		MK246858
<i>Schedorhinotermes</i> sp. 3	Khao Chong, Thailand	06-Nov-13	THAI063	JŠ		MK246856
<i>Schedorhinotermes</i> sp. 4	Milla Milla, Queensland, Australia	22-Jul-14	AUS104	JŠ		MK246837
<i>Schedorhinotermes</i> sp. 5	near Kuala Belait, Brunei	13-Feb	TBRU1.20	JŠ		MK246850

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<i>Schedorhinotermes</i> sp. 6	Darwin, Australia	12-Jun	AUS11	JŠ	MK246838
<i>Schedorhinotermes</i> sp. 7	Darwin, Australia	09-Feb-14	AUS61	JŠ	MK246839
<i>Schedorhinotermes</i> sp. 8	Cairns, Australia	16-Jul-14	AUS68	JŠ	MK246840
<i>Schedorhinotermes</i> sp. 9	near Kuala Belait, Brunei	13-Feb	TBRU5.4b	JŠ	MK246853
<i>Schedorhinotermes</i> sp. 10	Penang, Malaysia	13-Jul	TP1.25B	JŠ	MK246859
<i>Schedorhinotermes translucens</i>	Mac Ritchie, Singapore	12-Dec	T2.1d	JŠ	MK246847

Table S1. 2 PCR primers used in this study.

Primer name	Gene	Sequence (5' - 3')	Direction	Fragment size	Source
COIIF3150	COII	TGG CAG ATA AGT GCR BTG GAT TTA AG	Forward	10-kb fragment	Bourguignon et al. 2016
16R13687	16S	GAA GGG CCG CGG TAT TTT GAC C	Reverse	10-kb fragment	Bourguignon et al. 2016
16S13530F	16S	TWA AAC TCT ATA GGG TCT TCT CGT CCC A	Forward	6-kb fragment	Bourguignon et al. 2015
COII3810R	COII	TTT GCY CCR CAR ATT TCT GAG CAT TG	Reverse	6-kb fragment	Bourguignon et al. 2015

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Table S1. 3 Fossils used as calibrations for estimating divergence times among Rhinotermitinae lineages.

Species	Age (Myo)/minimum age constraint for group	Calibration group	Soft maximum bound (97.5% probability)	Reference	Comments on soft max. bound
<i>Mylacris anthracophila</i>	315	Dictyoptera + Phasmatodea	407	Scudder, 1868	First insect fossil (Engel and Grimaldi 2004)
<i>Juramantis initialis</i>	145	Dictyoptera	315.2	Vršanský, 2002	First cockroach fossils
<i>Valditermes brenanae</i>	130	Hodotermitidae + other Isoptera, excluding <i>Mastotermes</i>	235	Krishna et al. 2013 and references therein	<i>Triassoblatta argentina</i> , earliest fossil of Mesoblattinidae (Martins-Neto and Gallego 2005)
<i>Cratokalotermes santanensis</i>	112	Kalotermitidae + Rhinotermitidae + Termitidae	145	Grimaldi et al. 2008	Earliest fossil of termites
<i>Dolichorhinotermes dominicanus</i>	16	<i>Dolichorhinotermes</i> + <i>Rhinotermes</i>	94.3	Schlemmermeyer and Canello 2000	First fossil of Rhinotermitinae (Krishna and Grimaldi 2009)
<i>Reticulitermes antiquus</i>	33.9	<i>Reticulitermes</i> + <i>Coptotermes</i> + <i>Heterotermes</i>	94.3	Engel and Krishna 2007	First fossil of Rhinotermitinae (Krishna and Grimaldi 2009)
<i>Coptotermes sucineus</i>	16	<i>Coptotermes</i> + <i>Heterotermes</i>	33.9	Emerson 1971	First <i>Heterotermes</i> fossil

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<i>Constrictotermes electroconstrictus</i>	13.8	<i>Constrictotermes</i> + <i>Caetermes</i>	47.8	Krishna 1996	First fossil of Termitidae (Engel et al. 2011)
<i>Anoplotermes</i> sensu lato	13.8	All Apicotermitinae except <i>Jugositermes</i> and <i>Duplidentitermes</i>	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae (Engel et al. 2011)
<i>Microcerotermes insularis</i>	13.8	<i>Microcerotermes</i> + Syntermitinae	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae (Engel et al. 2011)
<i>Nanotermes</i>	47.8	Termitidae + <i>Coptotermes</i> + <i>Heterotermes</i> + <i>Reticulitermes</i>	94.3	Engel et al. 2011	First fossil of Rhinotermitinae (Krishna and Grimaldi 2009)
<i>Macrotermes pristinus</i>	16	<i>Macrotermes</i> + <i>Odontotermes</i> + <i>Synacanthotermes</i>	47.8	Charpentier 1843	First fossil of Termitidae (Engel et al. 2011)

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Table S2. 1 Samples used in this study with corresponding collection details and accession numbers.

Species	Family	Biogeographic realm	Collect locality	Collection code	Latitude	Longitude	Accession number	Reference
<i>Acorhinotermes subfusciceps</i>	Rhinotermitidae	Neotropical	Peru	PU799	-9.05222	-75.57818		
<i>Amitermes</i>	Termitidae	Nearctic	Texas, USA	US1193.3	29.4697	-100.95051		
<i>Anacanthotermes</i>	Hodotermitidae	Saharo-Arabian	Arava Desert	Anacanthotermes_w				
<i>Anacanthotermes</i>	Hodotermitidae	Saharo-Arabian	Bardala Jordan Valley	Anacanthotermes_s				
<i>Anacanthotermes</i>	Hodotermitidae	Saharo-Arabian	Iran	Iran 2b				
<i>Anoplotermes banksi</i>	Termitidae	Neotropical	Trinidad and	TT2170	10.664	-61.404		
<i>Archotermopsis Wroughtoni</i>	Archotermopsidae	Oriental		Archotermopsis Wroughtoni				
<i>Cahuallitermes intermedius</i>	Termitidae	Neotropical	Honduras	HN774	14.79912	-88.13399		
<i>Cahuallitermes</i> nr. <i>milleri</i>	Termitidae	Neotropical	Guatemala	GUA221	17.13716	-89.68039		
<i>Cavitermes tuberosus</i>	Termitidae	Neotropical	French Guiana	K100				
<i>Comatermes perfectus</i>	Kalotermitidae	Neotropical	Guadeloupe	GU815	16.18142	-61.73608		
<i>Constrictotermes cyphergaster</i>	Termitidae	Neotropical	Paraguay	PA766	-22.16223	-60.47436		
<i>Constrictotermes guantanamensis</i>	Termitidae	Neotropical	Cuba	CU1278	19.96407	-75.1017		
<i>Coptotermes testaceus</i>	Rhinotermitidae	Neotropical	Panama	PN159	-22.16223	-60.47436		
<i>Coptotermes testaceus</i>	Rhinotermitidae	Neotropical	Trinidad and	TT1880	10.1365	-61.07652		
<i>Cornitermes ovatus</i>	Termitidae	Neotropical	Paraguay	PA351	-22.67878	-55.99503		
<i>Cornitermes pugnax</i>	Termitidae	Neotropical	Peru	PU620	-8.37007	-74.84366		
<i>Cryptocercus punctulatus</i>	Cryptocercidae	Nearctic	Korea	Korea				

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<i>Cryptotermes bracketti</i>	Kalotermitidae	Neotropical	Bahamas	BA1848	24.10073	-74.44728		
<i>Cryptotermes parvifrons</i>	Kalotermitidae	Neotropical	Trinidad and	TT1023.1	10.68015	-61.62518		
<i>Curvitermes odontognathus</i>	Termitidae	Neotropical	Bolivia	BO209	24.10073	-74.44728		
<i>Dolichorhinotermes longilabius</i>	Rhinotermitidae	Neotropical	French Guiana	G454				
<i>Dolichorhinotermes tenebrosus</i>	Rhinotermitidae	Neotropical	Bolivia	BO1076	-18.10037	-63.59343		
<i>Embiraetermes parvirostris</i>	Termitidae	Neotropical	French Guiana	Nour 3-27 F				
<i>Glyptotermes barbouri</i>	Kalotermitidae	Neotropical	Venezuela	VZ397	10.33783	-67.65527		
<i>Gnathamitermes grandis</i>	Termitidae	Neotropical	Mexico	MX98	21.88558	-102.29335		
<i>Gnathamitermes nr. perplexus</i>	Termitidae	Nearctic	Texas, USA	US512	30.59513	-103.92287		
<i>Heterotermes convexinotatus</i>	Rhinotermitidae	Neotropical	Puerto Rico	PR182	17.93333	-66.15		
<i>Heterotermes tenuis</i>	Rhinotermitidae	Neotropical	Paraguay	PA248	-23.71941	-56.48601		
<i>Hodotermes</i>	Hodotermitidae	Afrotropical	South Africa	SA16_13				
<i>Hodotermes mossambicus</i>	Hodotermitidae	Afrotropical	Namibia	Nam 18 PG 095				
<i>Hodotermes mossambicus</i>	Hodotermitidae	Afrotropical	South Africa	AFR111	-30.783	28.583		
<i>Hodotermes mossambicus</i>	Hodotermitidae	Afrotropical		AFR 131.0				
<i>Hodotermopsis sjostedti</i>	Archotermopsidae	Oriental	China	HSRNA1				
<i>Hodotermopsis sjostedti</i>	Archotermopsidae	Oriental	Yakushima Island, Japan				KP026259	Bourguignon et al. 2015
<i>Incisitermes schwarzi</i>	Kalotermitidae	Neotropical	Colombia	CO497.1	10.97048	-74.37705		
<i>Mastotermes darwiniensis</i>	Mastotermitidae	Australian	Australia	MD-RNA-1				
<i>Mastotermes darwiniensis</i>	Mastotermitidae	Australian	Darwin, NT,				JX144929	Cameron et al. 2012
<i>Microcerotermes arboreus</i>	Termitidae	Neotropical	Trinidad and	TT2014	10.46736	-61.12253		
<i>Microcerotermes bouvieri</i>	Termitidae	Neotropical	Venezuela	VZ124	10.20256	-65.68809		
<i>Microhodotermes viator</i>	Hodotermitidae	Afrotropical	Worcester, South Africa				JX144931	Cameron et al. 2012

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<i>Neotermes setifer</i>	Kalotermitidae	Neotropical	Panama	PN661	9.26399	-79.93746		
<i>Orthognathotermes</i>	Termitidae	Neotropical	Ecuador	EC986	-0.67177	-76.39793		
<i>Orthognathotermes n. sp.</i>	Termitidae	Neotropical	Paraguay	PA360	-22.67878	-55.99503		
<i>Porotermes</i>	Stolotermitidae	Afrotropical	South Africa	POROTERMES52				
<i>Porotermes adamsoni</i>	Stolotermitidae	Australian	Australia	Aus19	-33.04558236	151.3263299		
<i>Porotermes adamsoni</i>	Stolotermitidae	Australian	Glen Elgin State Forest, NSW,				JX144930	Cameron et al. 2012
<i>Porotermes quadricollis</i>	Stolotermitidae	Neotropical	Chile	PORO-CHILI				
<i>Reticulitermes catalinensis</i>	Rhinotermitidae	Nearctic	California, USA	US430	33.32298	-118.34468		
<i>Reticulitermes virginicus</i>	Rhinotermitidae	Nearctic	Florida, USA	FL395	26.4445	-81.43383		
<i>Rhinotermes hispidus</i>	Rhinotermitidae	Neotropical	Ecuador	EC1239	-0.67177	-76.39793		
<i>Rhinotermes marginalis</i>	Rhinotermitidae	Neotropical	Ecuador	EC398	19.96407	-75.1017		
<i>Rugitermes flavicinctus</i>	Kalotermitidae	Neotropical	Trinidad and	TT342.1	10.79817	-61.35		
<i>Stolotermes inopinus</i>	Stolotermitidae	New Zealand	New Zealand	Log8				
<i>Stolotermes ruficeps</i>	Stolotermitidae	New Zealand	New Zealand	AUS18	-35.24167	173.92583		
<i>Stolotermes ruficeps</i>	Stolotermitidae	New Zealand	New Zealand					
<i>Stolotermes victoriensis</i>	Stolotermitidae	Australian	Australia	AUS19	-33.04558236	151.3263299		
<i>Stolotermes victoriensis</i>	Stolotermitidae	Australian	Australia	AUST14-12				
<i>Zootermopsis angusticollis</i>	Archotermopsidae	Nearctic	California, USA	US1615	37.373719	-122.117781		
<i>Zootermopsis angusticollis</i>	Archotermopsidae	Nearctic	California, USA	US731	32.67122	-116.82597		
<i>Zootermopsis angusticollis</i>	Archotermopsidae	Nearctic	Triangle Mountain, British Columbia, Canada	Canada			JX144932	Cameron et al. 2012
<i>Zootermopsis laticeps</i>	Archotermopsidae	Nearctic	New Mexico, USA	US1112	35.1133	-106.60403		

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<i>Zootermopsis nevadensis</i>	Archotermopsidae	Nearctic	California, USA		36.36408	-121.5554	KJ958410	Qian 2014
<i>Zootermopsis nevadensis</i>	Archotermopsidae	Nearctic	California, USA	US564	39.21477	-121.05674		
<i>Zootermopsis nevadensis</i>	Archotermopsidae	Nearctic		US17	31.35	-110.25		

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Table S2. 2 Fossils used for time calibration in this study

Fossil species	Minimum age constraint (MY)	Calibration group	Soft maximum bound (97.5% probability)	Reference	Note on maximum bound
<i>Melqartitermes myrrheus</i>	125.45	Mastotermitidae + sister group	235	Engel et al. 2007	<i>Triassoblatta argentina</i> , earliest fossil of Mesoblattinidae (Martins-Neto et al. 2005)
<i>Cosmotermes multus</i>	94.3	Stolotermitidae + Hodotermitidae + Archotermopsidae	235	Zhao et al. 2019	<i>Triassoblatta argentina</i> , earliest fossil of Mesoblattinidae (Martins-Neto et al. 2005)
<i>Archeorhinotermes rossi</i>	94.3	Neoisoptera + Kalotermitidae	235	Krishna and Grimaldi 2003	<i>Triassoblatta argentina</i> , earliest fossil of Mesoblattinidae (Martins-Neto et al. 2005)
<i>Nanotermes isaacae</i>	47.8	Termitidae + <i>Coptotermes</i> + <i>Heterotermes</i> + <i>Reticulitermes</i>	94.3	Engel et al. 2011	First fossil of Rhinotermitinae
<i>Reticulitermes antiquus</i>	33.9	<i>Reticulitermes</i> + <i>Coptotermes</i> + <i>Heterotermes</i>	94.3	Engel et al. 2007	First fossil of Rhinotermitinae
<i>Dolichorhinotermes dominicanus</i>	16	<i>Dolichorhinotermes</i> + <i>Rhinotermes</i> + <i>Accorhinotermes</i>	94.3	Schlemmermeyer and Canello 2000	First fossil of Rhinotermitinae
<i>Coptotermes sucineus</i>	16	<i>Coptotermes testaceus</i> + <i>Heterotermes tenuis</i> + <i>Heterotermes convexinotatus</i>	33.9	Engel 2008	First <i>Heterotermes</i> fossil
<i>Constrictotermes electroconstrictus</i>	13.8	<i>Constrictotermes</i> + sister group	47.8	Krishna 1996	First fossil of Termitidae
<i>Microcerotermes insularis</i>	13.8	<i>Microcerotermes</i> + Syntermitinae	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae
<i>Amitermes lucidus</i>	13.8	<i>Amitermes</i> + <i>Drepanotermes</i> + <i>Orthognathotermes</i>	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae

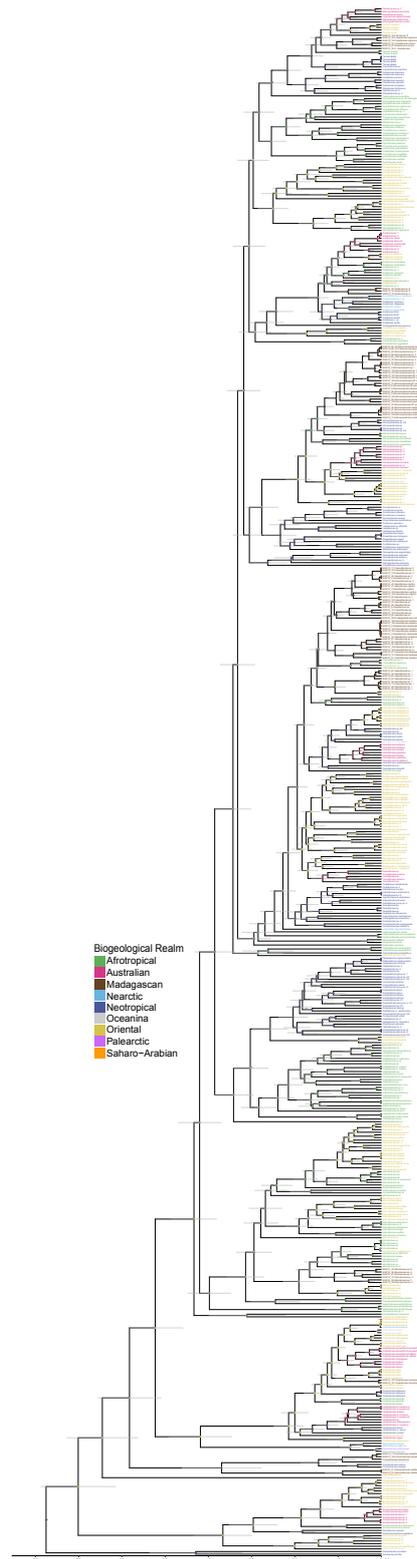


Figure S3. 1 Time-calibrated phylogenetic tree of Neoisoptera reconstructed with BEAST2 using mitochondrial genomes without third codon positions.

The ancestral range reconstruction was performed with the best-fit model (see Table S3.3): the DIVALIKE+J mode of BioGeoBEARS. Node bars indicate the 95% HPD intervals. Posterior probabilities are indicated for nodes with support < 0.9. Pie charts on the nodes show the reconstructed ancestral ranges. Colors represent the biogeographical realms recognized in this study (see Holt et al. 2013).

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Figure S3. 2 Time-calibrated phylogenetic tree of Neoisoptera reconstructed with BEAST2 using mitochondrial genomes with third codon positions included.

The ancestral range reconstruction was performed with the best-fit model (see Table S3.3): the DEC+J model of BioGeoBEARS. Node bars indicate the 95% HPD intervals. Posterior probabilities are indicated for nodes with support < 0.9. Pie charts on the nodes show the reconstructed ancestral ranges. Colors represent the biogeographical realms recognized in this study (see Holt et al. 2013).

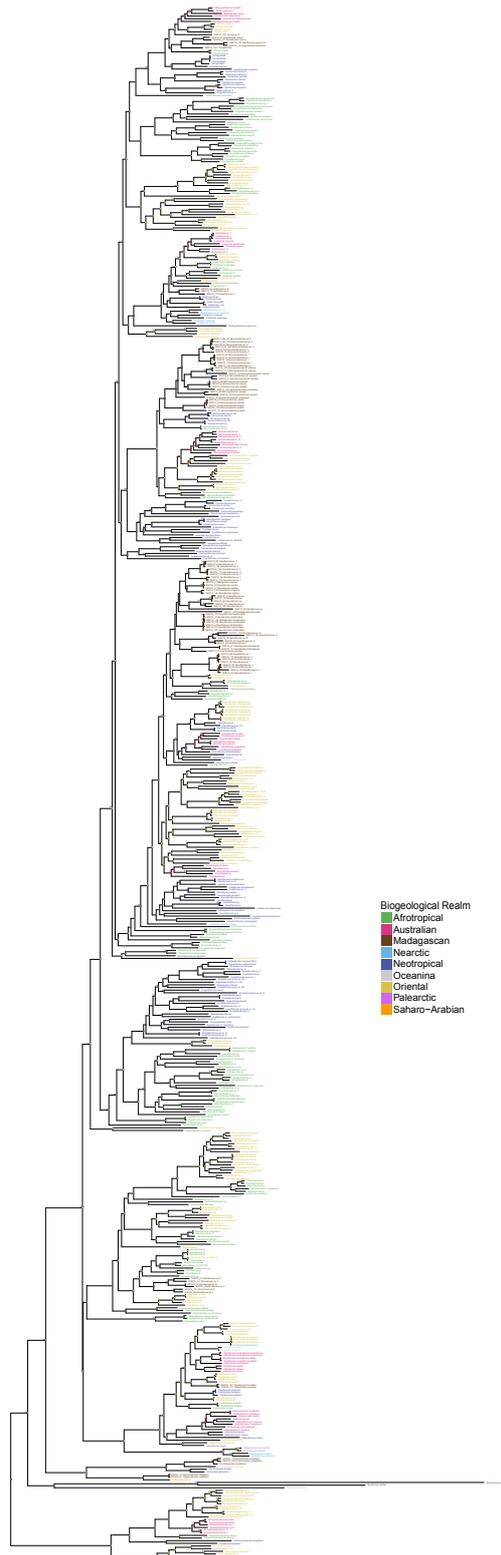


Figure S3. 3 Maximum likelihood phylogenetic tree of Neoisoptera reconstructed with IQ-TREE using mitochondrial genomes without third codon positions.

The ancestral range reconstruction was performed with the best-fit model (see Table S3.3): the DEC+J model of BioGeoBEARS. Node bars indicate the 95% HPD intervals. Posterior probabilities are indicated for nodes with support < 0.9. Pie charts on the nodes show the reconstructed ancestral ranges. Colors represent the biogeographical realms recognized in this study (see Holt et al. 2013).

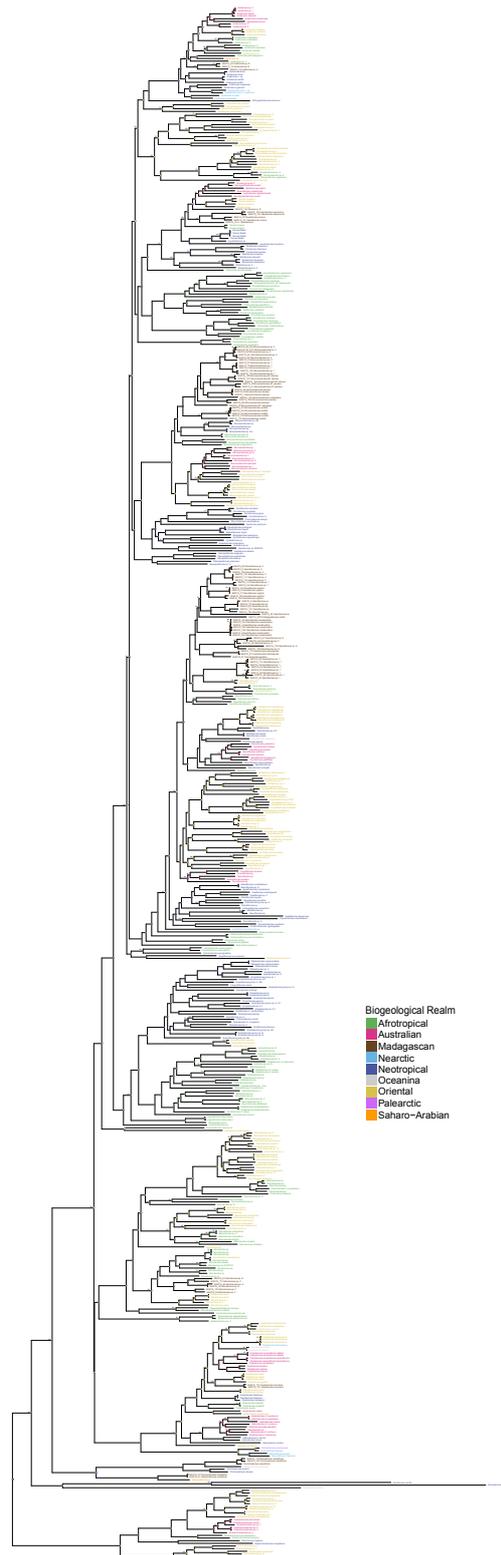


Figure S3. 4 Maximum likelihood phylogenetic tree of Neoisoptera reconstructed with IQ-TREE using mitochondrial genomes with third codon positions included.

The ancestral range reconstruction was performed with the best-fit model (see Table S3.3): the DEC+J model of BioGeoBEARS. Node bars indicate the 95% HPD intervals. Posterior probabilities are indicated for nodes with support < 0.9. Pie charts on the nodes show the reconstructed ancestral ranges. Colors represent the biogeographical realms recognized in this study (see Holt et al. 2013).

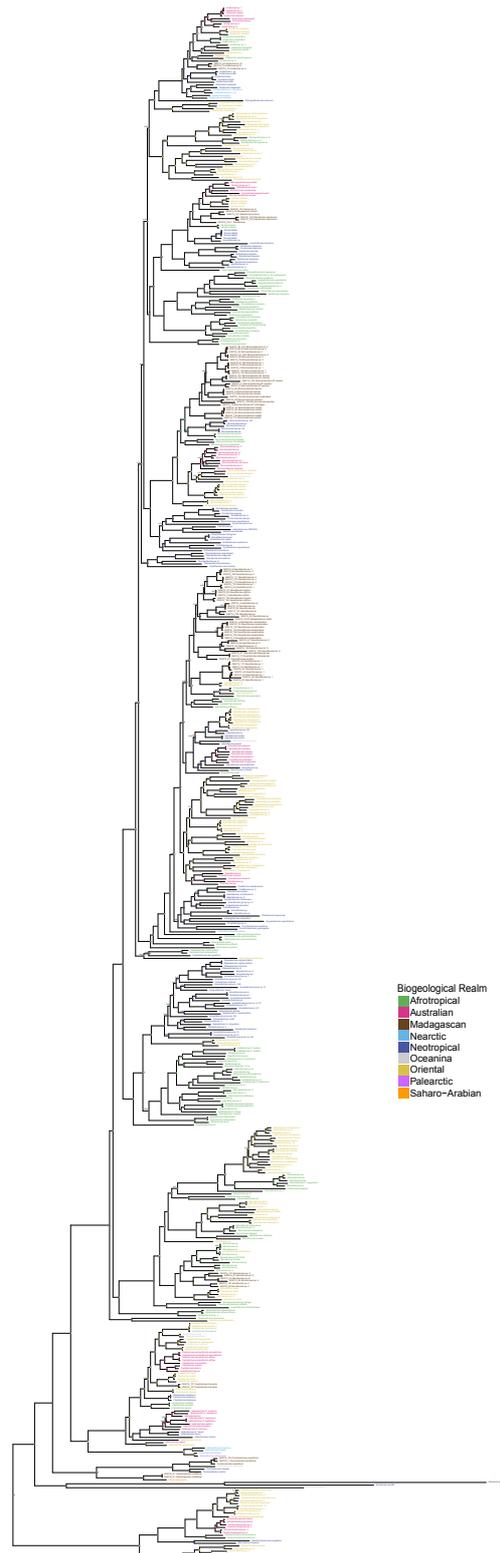


Figure S3. 5 Bayesian phylogenetic tree of Neoisoptera reconstructed with MrBayes using mitochondrial genomes without third codon positions.

The ancestral range reconstruction was performed with the best-fit model (see Table 3.3): the DIVALIKE+J model of BioGeoBEARS. Node bars indicate the 95% HPD intervals. Posterior probabilities are indicated for nodes with support < 0.9. Stars indicate unresolved polytomies in the original MrBayes tree. Pie charts on the nodes show the reconstructed ancestral ranges. Colors represent the biogeographical realms recognized in this study (see Holt et al. 2013).

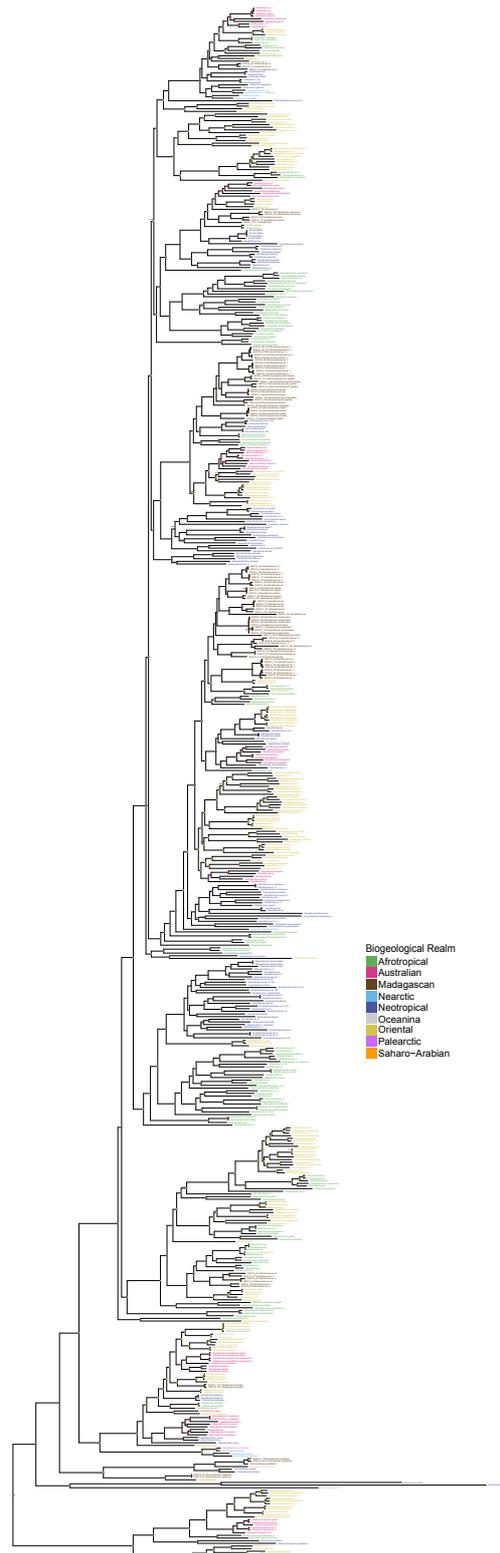


Figure S3. 6 Bayesian phylogenetic tree of Neoisoptera reconstructed with MrBayes using mitochondrial genomes without third codon positions.

The ancestral range reconstruction was performed with the best-fit model (see Table 3.3): the DIVALIKE+J model of BioGeoBEARS. Node bars indicate the 95% HPD intervals. Posterior probabilities are indicated for nodes with support < 0.9. Stars indicate unresolved polytomies in the original MrBayes tree. Pie charts on the nodes show the reconstructed ancestral ranges. Colors represent the biogeographical realms recognized in this study (see Holt et al. 2013).

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Table S3. 1 Samples used in this study, with corresponding collection details and accession numbers.

species	Family	Biogeological Realms	Accession Number	Reference
<i>Acanthotermes acanthothorax</i>	Termitidae	Afrotropic	KP026280.1	Bourguignon et al. 2015
<i>Acholotermes chirotus</i>	Termitidae	Afrotropic	KY224688.1	Bourguignon et al. 2017
<i>Aciculitermes aciculatus</i>	Termitidae	Oriental	KY224548.1	Bourguignon et al. 2017
<i>Aciculitermes maymyoensis</i>	Termitidae	Oriental	KY224601.1	Bourguignon et al. 2017
<i>Aciculitermes</i> sp.	Termitidae	Oriental	KY224659.1	Bourguignon et al. 2017
<i>Acidnotermes praus</i>	Termitidae	Afrotropic	KY224646.1	Bourguignon et al. 2017
<i>Aderitotermes cf. fossor</i>	Termitidae	Afrotropic	KY224471.1	Bourguignon et al. 2017
<i>Aderitotermes</i> sp.	Termitidae	Afrotropic	KP026282.1	Bourguignon et al. 2015
<i>Aderitotermes</i> sp.	Termitidae	Afrotropic	KY224657.1	Bourguignon et al. 2017
<i>Aderitotermes</i> sp. 2	Termitidae	Afrotropic	KY224719.1	Bourguignon et al. 2017
<i>Agnathotermes crassinasus</i>	Termitidae	Neotropic	KY224404.1	Bourguignon et al. 2017
<i>Allodotermes schultzei</i>	Termitidae	Afrotropic	KY224522.1	Bourguignon et al. 2017
<i>Alyscotermes kilimandjaricus</i>	Termitidae	Afrotropic	KY224395.1	Bourguignon et al. 2017
<i>Alyscotermes</i> sp.	Termitidae	Afrotropic	KY224502.1	Bourguignon et al. 2017
<i>Alyscotermes</i> sp. B	Termitidae	Afrotropic	KY224687.1	Bourguignon et al. 2017
<i>Amalotermes phaeocephalus</i>	Termitidae	Afrotropic	KP026275.1	Bourguignon et al. 2015
<i>Amalotermes phaeocephalus</i>	Termitidae	Afrotropic	KY224574.1	Bourguignon et al. 2017
<i>Amitermes amifer</i>	Termitidae	Neotropic		ID by RH Scheffrahn
<i>Amitermes amifer</i>	Termitidae	Neotropic		ID by RH Scheffrahn
<i>Amitermes capito</i>	Termitidae	Australia	KY224432.1	Bourguignon et al. 2017
<i>Amitermes coachellae</i>	Termitidae	Nearctic		ID by RH Scheffrahn
<i>Amitermes cryptodon</i>	Termitidae	Neotropic		ID by RH Scheffrahn
<i>Amitermes dentatus</i>	Termitidae	Oriental	KY224513.1	Bourguignon et al. 2017
<i>Amitermes dentatus</i>	Termitidae	Oriental	KY224549.1	Bourguignon et al. 2017
<i>Amitermes dentatus</i>	Termitidae	Oriental	KY224593.1	Bourguignon et al. 2017
<i>Amitermes foreli</i>	Termitidae	Neotropic		ID by RH Scheffrahn
<i>Amitermes foreli</i>	Termitidae	Neotropic		
<i>Amitermes loennbergianus</i>	Termitidae	Afrotropic		
<i>Amitermes megaceps</i>	Termitidae	Neotropic		ID by RH Scheffrahn
<i>Amitermes meridionalis</i>	Termitidae	Australia	KY224487.1	Bourguignon et al. 2017
<i>Amitermes messinae</i>	Termitidae	Afrotropic		
<i>Amitermes</i> n. sp	Termitidae	Neotropic		ID by RH Scheffrahn
<i>Amitermes obeuntis</i>	Termitidae	Australia	KY224650.1	Bourguignon et al. 2017
<i>Amitermes snyderi</i>	Termitidae	Nearctic		ID by RH Scheffrahn

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<i>Amitermes</i> sp.	Termitidae	Saharo_Arabian		
<i>Amitermes</i> sp. 1	Termitidae	Australia	KY224629.1	Bourguignon et al. 2017
<i>Amitermes</i> sp. 2	Termitidae	Australia	KY224602.1	Bourguignon et al. 2017
<i>Amitermes</i> sp. 3	Termitidae	Afrotropic	KY224581.1	Bourguignon et al. 2017
<i>Amitermes</i> sp. 4	Termitidae	Afrotropic	KY224426.1	Bourguignon et al. 2017
<i>Amitermes</i> sp. 5	Termitidae	Afrotropic	KY224528.1	Bourguignon et al. 2017
<i>Amitermes</i> sp. A	Termitidae	Oriental	KY224621.1	Bourguignon et al. 2017
<i>Amitermes</i> sp. D	Termitidae	Australia	KY224695.1	Bourguignon et al. 2017
<i>Amitermes</i> sp. E	Termitidae	Australia	KY224564.1	Bourguignon et al. 2017
<i>Amitermes spinifer</i>	Termitidae	Afrotropic		
<i>Amitermes unidentatus</i>	Termitidae	Afrotropic		
<i>Amitermes unidentatus</i>	Termitidae	Afrotropic		
<i>Ancistrotermes pakistanicus</i>	Termitidae	Oriental	KP026267.1	Bourguignon et al. 2015
<i>Anenteotermes</i> cf. <i>polyscolus</i>	Termitidae	Afrotropic	KY224577.1	Bourguignon et al. 2017
<i>Angularitermes nasutissimus</i>	Termitidae	Neotropic	KY224640.1	Bourguignon et al. 2017
<i>Anhangatermes macarthuri</i>	Termitidae	Neotropic	KY224556.1	Bourguignon et al. 2017
<i>Anoplotermes banksi</i>	Termitidae	Neotropic	KY224509.1	Bourguignon et al. 2017
<i>Anoplotermes</i> group nr. AB	Termitidae	Neotropic	KY224668.1	Bourguignon et al. 2017
<i>Anoplotermes</i> group sp. 1	Termitidae	Neotropic	KY224469.1	Bourguignon et al. 2017
<i>Anoplotermes</i> group sp. AD	Termitidae	Neotropic	KY224450.1	Bourguignon et al. 2017
<i>Anoplotermes</i> group sp. AF	Termitidae	Neotropic	KY224670.1	Bourguignon et al. 2017
<i>Anoplotermes</i> group sp. N	Termitidae	Neotropic	KY224480.1	Bourguignon et al. 2017
<i>Anoplotermes</i> group sp. N	Termitidae	Neotropic	KY224685.1	Bourguignon et al. 2017
<i>Anoplotermes</i> group sp. nr. E1	Termitidae	Neotropic	KP026287.1	Bourguignon et al. 2015
<i>Anoplotermes</i> group sp. Q	Termitidae	Neotropic	KY224540.1	Bourguignon et al. 2017
<i>Anoplotermes</i> group sp. SB	Termitidae	Neotropic	KY224399.1	Bourguignon et al. 2017
<i>Anoplotermes janus</i>	Termitidae	Neotropic	KY224641.1	Bourguignon et al. 2017
<i>Anoplotermes janus</i>	Termitidae	Neotropic	KY224653.1	Bourguignon et al. 2017
<i>Anoplotermes parvus</i>	Termitidae	Neotropic	KY224649.1	Bourguignon et al. 2017
<i>Anoplotermes</i> sp.	Termitidae	Neotropic	KY224424.1	Bourguignon et al. 2017
<i>Anoplotermes</i> sp. E1	Termitidae	Neotropic	KY224415.1	Bourguignon et al. 2017
<i>Anoplotermes</i> sp. E1	Termitidae	Neotropic	KY224720.1	Bourguignon et al. 2017
<i>Aparatermes</i> nr. <i>cingulatus</i>	Termitidae	Neotropic	KY224484.1	Bourguignon et al. 2017
<i>Aparatermes</i> sp. A	Termitidae	Neotropic	KY224536.1	Bourguignon et al. 2017
<i>Aparatermes</i> sp. A	Termitidae	Neotropic	KY224575.1	Bourguignon et al. 2017
Apicotermatinae gen. A sp.	Termitidae	Afrotropic	KY224459.1	Bourguignon et al. 2017
<i>Apilitermes longiceps</i>	Termitidae	Afrotropic	KY224419.1	Bourguignon et al. 2017

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<i>Araujotermes parvulus</i>	Termitidae	Neotropic	KY224477.1	Bourguignon et al. 2017
<i>Astalotermes cf. obstructus</i>	Termitidae	Afrotropic	KY224700.1	Bourguignon et al. 2017
<i>Astalotermes cf. quietus</i>	Termitidae	Afrotropic	KY224465.1	Bourguignon et al. 2017
<i>Astalotermes cf. quietus</i>	Termitidae	Afrotropic	KY224400.1	Bourguignon et al. 2017
<i>Astalotermes murcus</i>	Termitidae	Afrotropic	KY224676.1	Bourguignon et al. 2017
<i>Astalotermes sp.</i>	Termitidae	Afrotropic	KY224462.1	Bourguignon et al. 2017
<i>Astalotermes sp.</i>	Termitidae	Afrotropic	KP026272.1	Bourguignon et al. 2015
<i>Astalotermes sp. B</i>	Termitidae	Afrotropic	KY224505.1	Bourguignon et al. 2017
<i>Astratotermes sp.</i>	Termitidae	Afrotropic	KY224418.1	Bourguignon et al. 2017
<i>Astratotermes sp. A</i>	Termitidae	Afrotropic	KY224455.1	Bourguignon et al. 2017
<i>Ateuchotermes retifaciens</i>	Termitidae	Afrotropic	KY224497.1	Bourguignon et al. 2017
<i>Ateuchotermes sp.</i>	Termitidae	Afrotropic	KP026274.1	Bourguignon et al. 2015
<i>Ateuchotermes sp. C</i>	Termitidae	Afrotropic	KY224672.1	Bourguignon et al. 2017
<i>Ateuchotermes sp. C</i>	Termitidae	Afrotropic	KY224674.1	Bourguignon et al. 2017
<i>Atlantitermes oculatissimus</i>	Termitidae	Neotropic	KY224728.1	Bourguignon et al. 2017
<i>Atlantitermes snyderi</i>	Termitidae	Neotropic	KY224583.1	Bourguignon et al. 2017
<i>Atlantitermes sp. D</i>	Termitidae	Neotropic	KY224547.1	Bourguignon et al. 2017
<i>Basidentitermes aurivillii</i>	Termitidae	Afrotropic	KP026281.1	Bourguignon et al. 2015
<i>Bulbitermes laticephalus</i>	Termitidae	Oriental	KY224481.1	Bourguignon et al. 2017
<i>Bulbitermes makhamensis</i>	Termitidae	Oriental	KY224413.1	Bourguignon et al. 2017
<i>Bulbitermes nr. laticephalus</i>	Termitidae	Oriental	KY224479.1	Bourguignon et al. 2017
<i>Bulbitermes sarawakensis</i>	Termitidae	Oriental	KY224451.1	Bourguignon et al. 2017
<i>Bulbitermes singaporiensis</i>	Termitidae	Oriental	KY224725.1	Bourguignon et al. 2017
<i>Bulbitermes sp. A</i>	Termitidae	Oriental	KY224544.1	Bourguignon et al. 2017
<i>Bulbitermes sp. B</i>	Termitidae	Oriental	KY224499.1	Bourguignon et al. 2017
<i>Bulbitermes sp. D</i>	Termitidae	Oriental	KY224598.1	Bourguignon et al. 2017
<i>Caetetermes taquarussu</i>	Termitidae	Neotropic	KP026285.1	Bourguignon et al. 2015
<i>Cavitermes parmae</i>	Termitidae	Neotropic	KY224712.1	Bourguignon et al. 2017
<i>Cavitermes tuberosus</i>	Termitidae	Neotropic	KP026294.1	Bourguignon et al. 2015
<i>Cavitermes tuberosus</i>	Termitidae	Neotropic	KY224568.1	Bourguignon et al. 2017
<i>Cephalotermes rectangularis</i>	Termitidae	Afrotropic	KP026277.1	Bourguignon et al. 2015
<i>Cephalotermes rectangularis</i>	Termitidae	Afrotropic	KY224689.1	Bourguignon et al. 2017
<i>Coatitermes kartaboensis</i>	Termitidae	Neotropic	KY224708.1	Bourguignon et al. 2017
<i>Coatitermes sp. 2</i>	Termitidae	Neotropic	KY224651.1	Bourguignon et al. 2017
<i>Compositermes vindai</i>	Termitidae	Neotropic	KY224716.1	Bourguignon et al. 2017
<i>Constrictotermes cavifrons</i>	Termitidae	Neotropic	KP026290.1	Bourguignon et al. 2015
<i>Constrictotermes cyphergaster</i>	Termitidae	Neotropic	KY224443.1	Bourguignon et al. 2017

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<i>Coptotermes acinaciformis acinaciformis</i>	Rhinotermitidae	Australia	KU925199.1	Bourguignon et al. 2016
<i>Coptotermes acinaciformis acinaciformis</i>	Rhinotermitidae	Australia	KU925198.1	Bourguignon et al. 2016
<i>Coptotermes acinaciformis raffrayi</i>	Rhinotermitidae	Australia	KU925196.1	Bourguignon et al. 2016
<i>Coptotermes acinaciformis raffrayi</i>	Rhinotermitidae	Australia	KU925197.1	Bourguignon et al. 2016
<i>Coptotermes amanii</i>	Rhinotermitidae	Afrotropic	KU925200.1	Bourguignon et al. 2016
<i>Coptotermes elisae</i>	Rhinotermitidae	Oceanic	KU925202.1	Bourguignon et al. 2016
<i>Coptotermes elisae</i>	Rhinotermitidae	Oceanic	KU925201.1	Bourguignon et al. 2016
<i>Coptotermes formosanus</i>	Rhinotermitidae	Nearctic	KU925203.1	Bourguignon et al. 2016
<i>Coptotermes formosanus</i>	Rhinotermitidae	Oriental	AB626145.1	Tokuda et al. 2011
<i>Coptotermes formosanus</i>	Rhinotermitidae	Oriental	AB626146	Tokuda et al. 2011
<i>Coptotermes formosanus</i>	Rhinotermitidae	Oriental	AB626147	Tokuda et al. 2011
<i>Coptotermes frenchi</i>	Rhinotermitidae	Australia	KU925204.1	Bourguignon et al. 2016
<i>Coptotermes gestroi</i>	Rhinotermitidae	Oriental	KU925205.1	Bourguignon et al. 2016
<i>Coptotermes heimi</i>	Rhinotermitidae	Oriental	KU925206.1	Bourguignon et al. 2016
<i>Coptotermes heimi</i>	Rhinotermitidae	Oriental	KU925207.1	Bourguignon et al. 2016
<i>Coptotermes heimi</i>	Rhinotermitidae	Oriental	KU925208.1	Bourguignon et al. 2016
<i>Coptotermes kalshoveni</i>	Rhinotermitidae	Oriental	KU925209.1	Bourguignon et al. 2016
<i>Coptotermes kalshoveni</i>	Rhinotermitidae	Oriental	KU925210.1	Bourguignon et al. 2016
<i>Coptotermes lacteus</i>	Rhinotermitidae	Australia	KU925211.1	Bourguignon et al. 2016
<i>Coptotermes lacteus</i>	Rhinotermitidae	Australia	JX144934.1	Cameron et al. 2012
<i>Coptotermes michaelsoni</i>	Rhinotermitidae	Australia	KU925212.1	Bourguignon et al. 2016
<i>Coptotermes remotus</i>	Rhinotermitidae	Oceanic	KU925213.1	Bourguignon et al. 2016
<i>Coptotermes sepangensis</i>	Rhinotermitidae	Oriental	KU925214.1	Bourguignon et al. 2016
<i>Coptotermes sepangensis</i>	Rhinotermitidae	Oriental	KU925215.1	Bourguignon et al. 2016
<i>Coptotermes sjostedti</i>	Rhinotermitidae	Afrotropic	KU925216.1	Bourguignon et al. 2016
<i>Coptotermes sjostedti</i>	Rhinotermitidae	Afrotropic	KU925217.1	Bourguignon et al. 2016
<i>Coptotermes testaceus</i>	Rhinotermitidae	Neotropic	KU925218.1	Bourguignon et al. 2016
<i>Coptotermes testaceus</i>	Rhinotermitidae	Neotropic	KU925219.1	Bourguignon et al. 2016
<i>Coptotermes testaceus</i>	Rhinotermitidae	Neotropic	KU925220.1	Bourguignon et al. 2016
<i>Coptotermes travians</i>	Rhinotermitidae	Oriental	KU925221.1	Bourguignon et al. 2016
<i>Coptotermes travians</i>	Rhinotermitidae	Oriental	KU925222.1	Bourguignon et al. 2016
<i>Cornitermes cumulans</i>	Termitidae	Neotropic	KY224411.1	Bourguignon et al. 2017
<i>Cornitermes cumulans</i>	Termitidae	Neotropic	KY224538.1	Bourguignon et al. 2017
<i>Cornitermes pugnax</i>	Termitidae	Neotropic	KY224474.1	Bourguignon et al. 2017
<i>Cornitermes</i> sp. A	Termitidae	Neotropic	KY224702.1	Bourguignon et al. 2017
<i>Crenetermes albotarsalis</i>	Termitidae	Afrotropic	KY224620.1	Bourguignon et al. 2017
<i>Crepititermes verruculosus</i>	Termitidae	Neotropic	KY224440.1	Bourguignon et al. 2017

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<i>Cryptocercus relictus</i>	Cryptocercidae	Afrotropic	JX144941.1	Cameron et al. 2012
<i>Cryptotermes secundus</i>	Kalotermitidae	Australia	KP026283.1	Bourguignon et al. 2015
<i>Cylindrotermes parvignathus</i>	Termitidae	Neotropic	KY224565.1	Bourguignon et al. 2017
<i>Cyrrillotermes angulariceps</i>	Termitidae	Neotropic	KY224613.1	Bourguignon et al. 2017
<i>Cyrrillotermes</i> sp.	Termitidae	Neotropic	KY224627.1	Bourguignon et al. 2017
<i>Dicuspiditermes nemorosus</i>	Termitidae	Oriental	KY224516.1	Bourguignon et al. 2017
<i>Dicuspiditermes</i> sp. 2	Termitidae	Oriental	KY224591.1	Bourguignon et al. 2017
<i>Dihoplotermes</i> sp. A	Termitidae	Neotropic	KY224436.1	Bourguignon et al. 2017
<i>Diversitermes</i> sp. A	Termitidae	Neotropic	KY224671.1	Bourguignon et al. 2017
<i>Dolichorhinotermes longilabius</i>	Rhinotermitidae	Neotropic	KP026258.1	Bourguignon et al. 2015
<i>Drepanotermes</i> sp.	Termitidae	Australia	JX144938.1	Cameron et al. 2012
<i>Duplidentitermes</i> sp.	Termitidae	Afrotropic	KP026271.1	Bourguignon et al. 2015
<i>Embiratermes brevinasus</i>	Termitidae	Neotropic	KY224580.1	Bourguignon et al. 2017
<i>Embiratermes neotenicus</i>	Termitidae	Neotropic	KP026262.1	Bourguignon et al. 2015
<i>Ephelotermes melachoma</i>	Termitidae	Australia	KY224392.1	Bourguignon et al. 2017
<i>Ephelotermes taylori</i>	Termitidae	Australia	KY224729.1	Bourguignon et al. 2017
<i>Euhamitermes hamatus</i>	Termitidae	Oriental	KY224490.1	Bourguignon et al. 2017
<i>Euhamitermes hamatus</i>	Termitidae	Oriental	KY224652.1	Bourguignon et al. 2017
<i>Euhamitermes</i> sp. A	Termitidae	Oriental	KY224727.1	Bourguignon et al. 2017
<i>Eutermellus aquilinus</i>	Termitidae	Afrotropic		
<i>Foraminitermes rhinoceros</i>	Termitidae	Afrotropic	KY224630.1	Bourguignon et al. 2017
<i>Furculitermes cubitalis</i>	Termitidae	Afrotropic	KY224669.1	Bourguignon et al. 2017
<i>Furculitermes longilabius</i>	Termitidae	Afrotropic	KY224662.1	Bourguignon et al. 2017
<i>Furculitermes soyeri</i>	Termitidae	Afrotropic	KY224530.1	Bourguignon et al. 2017
<i>Furculitermes winifredae</i>	Termitidae	Afrotropic	KY224488.1	Bourguignon et al. 2017
<i>Globitermes globosus</i>	Termitidae	Oriental	KY224563.1	Bourguignon et al. 2017
<i>Globitermes sulphureus</i>	Termitidae	Oriental	KY224703.1	Bourguignon et al. 2017
<i>Glossotermes occulatus</i>	Serritermitidae	Neotropic	KP026291.1	Bourguignon et al. 2015
<i>Glyptotermes satsumensis</i>	Kalotermitidae	Oriental	KP026257.1	Bourguignon et al. 2015
<i>Glyptotermes</i> sp. A	Kalotermitidae	Neotropic	KP026263.1	Bourguignon et al. 2015
<i>Glyptotermes</i> sp. B	Kalotermitidae	Oriental	KP026301.1	Bourguignon et al. 2015
<i>Glyptotermes</i> sp. C	Kalotermitidae	Oriental	KP026300.1	Bourguignon et al. 2015
<i>Gnathamitermes</i> n. sp	Termitidae	Nearctic		ID by RH Scheffrahn
<i>Gnathamitermes</i> nr. <i>perplexus</i>	Termitidae	Nearctic		ID by RH Scheffrahn
<i>Havilanditermes atripennis</i>	Termitidae	Oriental	KY224473.1	Bourguignon et al. 2017
<i>Havilanditermes proatripennis</i>	Termitidae	Oriental	KY224498.1	Bourguignon et al. 2017
<i>Heterotermes</i> cf. <i>occiduus</i>	Rhinotermitidae	Australia	KU925229.1	Bourguignon et al. 2016

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<i>Heterotermes cf. occiduus</i>	Rhinotermitidae	Australia	KU925230.1	Bourguignon et al. 2016
<i>Heterotermes cf. paradoxus</i>	Rhinotermitidae	Australia	KU925223.1	Bourguignon et al. 2016
<i>Heterotermes cf. paradoxus</i>	Rhinotermitidae	Australia	KU925224.1	Bourguignon et al. 2016
<i>Heterotermes cf. paradoxus</i>	Rhinotermitidae	Australia	KU925225.1	Bourguignon et al. 2016
<i>Heterotermes crinitus</i>	Rhinotermitidae	Neotropic	KU925226.1	Bourguignon et al. 2016
<i>Heterotermes malabaricus</i>	Rhinotermitidae	Oriental	KU925227.1	Bourguignon et al. 2016
<i>Heterotermes nr. tenuis</i>	Rhinotermitidae	Neotropic	KU925228.1	Bourguignon et al. 2016
<i>Heterotermes platycephalus</i>	Rhinotermitidae	Australia	KU925231.1	Bourguignon et al. 2016
<i>Heterotermes</i> sp.	Rhinotermitidae	Australia	JX144936.1	Cameron et al. 2012
<i>Heterotermes tenuior</i>	Rhinotermitidae	Oriental	KU925232.1	Bourguignon et al. 2016
<i>Heterotermes tenuis</i>	Rhinotermitidae	Neotropic	KU925233.1	Bourguignon et al. 2016
<i>Heterotermes vagus</i>	Rhinotermitidae	Australia	KU925234.1	Bourguignon et al. 2016
<i>Heterotermes validus</i>	Rhinotermitidae	Australia	KU925235.1	Bourguignon et al. 2016
<i>Hirtitermes hirtiventris</i>	Termitidae	Oriental	KY224680.1	Bourguignon et al. 2017
<i>Hirtitermes</i> sp. A	Termitidae	Oriental	KY224555.1	Bourguignon et al. 2017
<i>Hodotermopsis sjostedti</i>	Archotermopsidae	Oriental	KP026259.1	Bourguignon et al. 2015
<i>Homallotermes foraminifer</i>	Termitidae	Oriental	KY224434.1	Bourguignon et al. 2017
<i>Hospitalitermes hospitalis</i>	Termitidae	Oriental	KY224508.1	Bourguignon et al. 2017
<i>Hospitalitermes hospitalis</i>	Termitidae	Oriental	KY224588.1	Bourguignon et al. 2017
<i>Hospitalitermes medioflavus</i>	Termitidae	Oriental	KY224683.1	Bourguignon et al. 2017
<i>Hospitalitermes</i> sp. A	Termitidae	Oriental	KY224566.1	Bourguignon et al. 2017
<i>Hospitalitermes</i> sp. C	Termitidae	Oriental	KY224485.1	Bourguignon et al. 2017
<i>Hospitalitermes</i> sp. D	Termitidae	Oriental	KY224391.1	Bourguignon et al. 2017
<i>Hospitalitermes</i> sp. PHI3	Termitidae	Oriental	KY224698.1	Bourguignon et al. 2017
<i>Humitermes krishnai</i>	Termitidae	Neotropic	KY224663.1	Bourguignon et al. 2017
<i>Hypotermes makhmensis</i>	Termitidae	Oriental	KY224429.1	Bourguignon et al. 2017
<i>Inquilinitermes inquilinus</i>	Termitidae	Neotropic	KY224634.1	Bourguignon et al. 2017
<i>Inquilinitermes</i> sp.	Termitidae	Neotropic	KY224464.1	Bourguignon et al. 2017
<i>Isognathotermes finitimus</i>	Termitidae	Afrotropic	KY224569.1	Bourguignon et al. 2017
<i>Isognathotermes</i> sp. C	Termitidae	Afrotropic	KP026265.1	Bourguignon et al. 2015
<i>Isognathotermes ugandensis</i>	Termitidae	Afrotropic	KY224661.1	Bourguignon et al. 2017
<i>Jugositermes tuberculatus</i>	Termitidae	Afrotropic	KP026269.1	Bourguignon et al. 2015
<i>Jugositermes tuberculatus</i>	Termitidae	Afrotropic	KY224532.1	Bourguignon et al. 2017
<i>Kemneritermes sarawakensis</i>	Termitidae	Oriental	KY224410.1	Bourguignon et al. 2017
<i>Labiotermes labralis</i>	Termitidae	Neotropic	KP026292.1	Bourguignon et al. 2015
<i>Labiotermes</i> sp.	Termitidae	Neotropic	KY224468.1	Bourguignon et al. 2017
<i>Labiotermes</i> sp. BRA008	Termitidae	Neotropic	KY224605.1	Bourguignon et al. 2017

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<i>Labritermes buttelreepeni</i>	Termitidae	Oriental	KY224478.1	Bourguignon et al. 2017
<i>Leptomyxotermes doriae</i>	Termitidae	Afrotropic	KP026276.1	Bourguignon et al. 2015
<i>Leucopitermes leucops</i>	Termitidae	Oriental	KY224452.1	Bourguignon et al. 2017
<i>Longipeditermes longipes</i>	Termitidae	Oriental	KY224656.1	Bourguignon et al. 2017
<i>Longustitermes manni</i>	Termitidae	Neotropic	KY224558.1	Bourguignon et al. 2017
<i>Lophotermes septentrionalis</i>	Termitidae	Australia	KY224590.1	Bourguignon et al. 2017
<i>Macrognathotermes errator</i>	Termitidae	Australia	JX144939.1	Cameron et al. 2012
<i>Macrognathotermes sunteri</i>	Termitidae	Australia	KY224611.1	Bourguignon et al. 2017
<i>Macrotermes annandalei</i>	Termitidae	Oriental	KY224518.1	Bourguignon et al. 2017
<i>Macrotermes barneyi</i>	Termitidae	Oriental	JX050221.1	Cameron et al. 2012
<i>Macrotermes carbonarius</i>	Termitidae	Oriental	KY224449.1	Bourguignon et al. 2017
<i>Macrotermes carbonarius</i>	Termitidae	Oriental	KY224582.1	Bourguignon et al. 2017
<i>Macrotermes falciger</i>	Termitidae	Afrotropic	KY224460.1	Bourguignon et al. 2017
<i>Macrotermes gilvus</i>	Termitidae	Oriental	KY224607.1	Bourguignon et al. 2017
<i>Macrotermes gilvus</i>	Termitidae	Oriental	KY224691.1	Bourguignon et al. 2017
<i>Macrotermes malaccensis</i>	Termitidae	Oriental	KY224417.1	Bourguignon et al. 2017
<i>Macrotermes muelleri</i>	Termitidae	Afrotropic	KY224660.1	Bourguignon et al. 2017
<i>Macrotermes</i> sp.	Termitidae	Oriental	KY224521.1	Bourguignon et al. 2017
<i>Macrotermes</i> sp. A	Termitidae	Afrotropic	KY224531.1	Bourguignon et al. 2017
<i>Macrotermes</i> sp. B	Termitidae	Oriental	KY224525.1	Bourguignon et al. 2017
<i>Macrotermes subhyalinus</i>	Termitidae	Afrotropic	JX144937.1	Cameron et al. 2012
<i>Macrotermes subhyalinus</i>	Termitidae	Afrotropic	KY224559.1	Bourguignon et al. 2017
<i>Macrotermes vitrialatus</i>	Termitidae	Afrotropic	KY224472.1	Bourguignon et al. 2017
MAD15_100 <i>Protrichotermes canalifrons</i>	Rhinotermitidae	Madagascar		ID by SH MW
MAD15_104 <i>Microcerotermes unidentatus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_109 <i>Nasutitermes</i> sp. H	Termitidae	Madagascar		ID by SH MW
MAD15_114 <i>Microcerotermes subtilis</i>	Termitidae	Madagascar		ID by SH MW
MAD15_120 <i>Microtermes</i> sp. F	Termitidae	Madagascar		ID by SH MW
MAD15_121 <i>Coptotermes truncatus</i>	Rhinotermitidae	Madagascar		ID by SH MW
MAD15_124 <i>Termes</i> sp. B	Termitidae	Madagascar		ID by SH MW
MAD15_126 <i>Nasutitermes</i> sp.	Termitidae	Madagascar		ID by SH MW
MAD15_130 <i>Microcerotermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_131 <i>Microtermes</i> sp. C	Termitidae	Madagascar		ID by SH MW
MAD15_133 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_136 <i>Microcerotermes pauliani</i>	Termitidae	Madagascar		ID by SH MW
MAD15_138 <i>Nasutitermes</i> sp. G	Termitidae	Madagascar		ID by SH MW
MAD15_139 <i>Microcerotermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_141 <i>Nasutitermes</i> sp.	Termitidae	Madagascar		ID by SH MW

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MAD15_148 <i>Microcerotermes subtilis</i>	Termitidae	Madagascar		ID by SH MW
MAD15_152 <i>Nasutitermes nigrinus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_155 <i>Nasutitermes canaliculatus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_156 <i>Nasutitermes canaliculatus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_166 <i>Nasutitermes</i> sp. 3	Termitidae	Madagascar		ID by SH MW
MAD15_169 <i>Microcerotermes</i> aff. <i>sikorae</i>	Termitidae	Madagascar		ID by SH MW
MAD15_3 <i>Nasutitermes nigrinus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_33 <i>Nasutitermes canaliculatus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_36 <i>Microtermes</i> sp. A	Termitidae	Madagascar		ID by SH MW
MAD15_37 <i>Nasutitermes nigrinus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_38 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_39 <i>Microtermes</i> sp. B	Termitidae	Madagascar		ID by SH MW
MAD15_4 <i>Nasutitermes canaliculatus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_41 <i>Microcerotermes</i> aff. <i>pauliani</i>	Termitidae	Madagascar		ID by SH MW
MAD15_42 <i>Nasutitermes nigrinus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_43 <i>Microcerotermes subtilis</i>	Termitidae	Madagascar		ID by SH MW
MAD15_46 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_48 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_49 <i>Microcerotermes subtilis</i>	Termitidae	Madagascar		ID by SH MW
MAD15_54 <i>Microcerotermes</i> sp. 2	Termitidae	Madagascar		ID by SH MW
MAD15_57 <i>Microtermes</i> sp. D	Termitidae	Madagascar		ID by SH MW
MAD15_62 <i>Microcerotermes subtilis</i>	Termitidae	Madagascar		ID by SH MW
MAD15_63_S46 <i>Microcerotermes</i> sp. 2	Termitidae	Madagascar		ID by SH MW
MAD15_65 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_66 <i>Microcerotermes</i> sp. 2	Termitidae	Madagascar		ID by SH MW
MAD15_7 <i>Prorhinotermes canalifrons</i>	Rhinotermitidae	Madagascar		ID by SH MW
MAD15_72 <i>Amitermes</i> sp. A	Termitidae	Madagascar		ID by SH MW
MAD15_76 <i>Microcerotermes</i> sp. 2	Termitidae	Madagascar		ID by SH MW
MAD15_80 <i>Nasutitermes</i> sp.	Termitidae	Madagascar		ID by SH MW
MAD15_83 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_86_S10 <i>Microcerotermes</i> sp. 2	Termitidae	Madagascar		ID by SH MW
MAD15_86_S9 <i>Microcerotermes</i> sp. 2	Termitidae	Madagascar		ID by SH MW
MAD15_9 <i>Nasutitermes canaliculatus</i>	Termitidae	Madagascar		ID by SH MW
MAD15_93 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15_94 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD15-20 <i>Quasitermes incisus</i>	Termitidae	Madagascar		ID by SH MW
MAD15-5 <i>Microcerotermes</i> aff. <i>pauliani</i>	Termitidae	Madagascar		ID by SH MW
MAD19_100 <i>Microcerotermes</i> aff. <i>sikorae</i>	Termitidae	Madagascar		ID by SH MW
MAD19_103 <i>Nasutitermes</i> sp. 3	Termitidae	Madagascar		ID by SH MW

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MAD19_104 <i>Nasutitermes canaliculatus</i>	Termitidae	Madagascar		ID by SH MW
MAD19_107 <i>Coptotermes truncatus</i>	Rhinotermitidae	Madagascar		ID by SH MW
MAD19_108 <i>Nasutitermes nigritus</i>	Termitidae	Madagascar		ID by SH MW
MAD19_111 <i>Nasutitermes</i> sp. 3	Termitidae	Madagascar		ID by SH MW
MAD19_112 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD19_119 <i>Nasutitermes</i> sp. 3	Termitidae	Madagascar		ID by SH MW
MAD19_12 <i>Coactotermes baharaensis</i>	Termitidae	Madagascar		ID by SH MW
MAD19_121 <i>Microcerotermes</i> aff. <i>sikorae</i>	Termitidae	Madagascar		ID by SH MW
MAD19_122 <i>Nasutitermes canaliculatus</i>	Termitidae	Madagascar		ID by SH MW
MAD19_144 <i>Capritermes capricornis</i>	Termitidae	Madagascar		ID by SH MW
MAD19_150 <i>Capritermes capricornis</i>	Termitidae	Madagascar		ID by SH MW
MAD19_151 <i>Quasitermes incisus</i>	Termitidae	Madagascar		ID by SH MW
MAD19_19 <i>Amitermes</i> sp. B	Termitidae	Madagascar		ID by SH MW
MAD19_2 <i>Microcerotermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD19_27 <i>Psammotermes voeltzkowi</i>	Rhinotermitidae	Madagascar		ID by SH MW
MAD19_3 <i>Microcerotermes sikorae</i>	Termitidae	Madagascar		ID by SH MW
MAD19_39YR <i>Malagasitermes milloti</i>	Termitidae	Madagascar		ID by SH MW
MAD19_48 <i>Nasutitermes</i> sp. D	Termitidae	Madagascar		ID by SH MW
MAD19_5 <i>Nasutitermes</i> sp. 3	Termitidae	Madagascar		ID by SH MW
MAD19_51 <i>Psammotermes voeltzkowi</i>	Rhinotermitidae	Madagascar		ID by SH MW
MAD19_6 <i>Nasutitermes</i> sp.	Termitidae	Madagascar		ID by SH MW
MAD19_60 <i>Nasutitermes</i> sp.	Termitidae	Madagascar		ID by SH MW
MAD19_66 <i>Nasutitermes</i> sp. F	Termitidae	Madagascar		ID by SH MW
MAD19_67 <i>Nasutitermes</i> sp. E	Termitidae	Madagascar		ID by SH MW
MAD19_68 <i>Microcerotermes pauliani</i>	Termitidae	Madagascar		ID by SH MW
MAD19_75 <i>Nasutitermes</i> sp.	Termitidae	Madagascar		ID by SH MW
MAD19_76 nr. <i>Quasitermes</i>	Termitidae	Madagascar		ID by SH MW
MAD19_78 <i>Microcerotermes</i> aff. <i>subinteger</i>	Termitidae	Madagascar		ID by SH MW
MAD19_79 <i>Microcerotermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD19_8 <i>Microcerotermes sikorae</i>	Termitidae	Madagascar		ID by SH MW
MAD19_81 <i>Coarctotermes pauliani</i>	Termitidae	Madagascar		ID by SH MW
MAD19_82 <i>Microtermes</i> sp. F	Termitidae	Madagascar		ID by SH MW
MAD19_86 <i>Microcerotermes sikorae</i>	Termitidae	Madagascar		ID by SH MW
MAD19_87 <i>Microcerotermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
MAD19_88 <i>Nasutitermes</i> sp. 3	Termitidae	Madagascar		ID by SH MW
MAD19_92 <i>Amitermes</i> sp. B	Termitidae	Madagascar		ID by SH MW
MAD19_97 <i>Coactotermes baharaensis</i>	Termitidae	Madagascar		ID by SH MW
MAD19_98 <i>Nasutitermes</i> sp. 1	Termitidae	Madagascar		ID by SH MW
<i>Mastotermes darwiniensis</i>	Mastotermitidae	Australia	JX144929.1	Cameron et al. 2012

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<i>Microcerotermes baluchistanicus</i>	Termitidae	Oriental	KY224491.1	Bourguignon et al. 2017
<i>Microcerotermes biroi</i>	Termitidae	Oceanic	KP026297.1	Bourguignon et al. 2015
<i>Microcerotermes crassus</i>	Termitidae	Oriental	KY224428.1	Bourguignon et al. 2017
<i>Microcerotermes crassus</i>	Termitidae	Oriental	KY224445.1	Bourguignon et al. 2017
<i>Microcerotermes crassus</i>	Termitidae	Oriental	KY224461.1	Bourguignon et al. 2017
<i>Microcerotermes crassus</i>	Termitidae	Oriental	KY224496.1	Bourguignon et al. 2017
<i>Microcerotermes crassus</i>	Termitidae	Oriental	KY224690.1	Bourguignon et al. 2017
<i>Microcerotermes fuscotibialis</i>	Termitidae	Afrotropic	KY224494.1	Bourguignon et al. 2017
<i>Microcerotermes fuscotibialis</i>	Termitidae	Afrotropic	KY224645.1	Bourguignon et al. 2017
<i>Microcerotermes havilandi</i>	Termitidae	Oriental	KY224533.1	Bourguignon et al. 2017
<i>Microcerotermes nervosus</i>	Termitidae	Australia	KY224586.1	Bourguignon et al. 2017
<i>Microcerotermes newmani</i>	Termitidae	Australia	KY224394.1	Bourguignon et al. 2017
<i>Microcerotermes nr. havilandi</i>	Termitidae	Oriental	KY224610.1	Bourguignon et al. 2017
<i>Microcerotermes parvus</i>	Termitidae	Afrotropic	KY224448.1	Bourguignon et al. 2017
<i>Microcerotermes parvus</i>	Termitidae	Afrotropic	KY224699.1	Bourguignon et al. 2017
<i>Microcerotermes progreadiens</i>	Termitidae	Afrotropic	KY224679.1	Bourguignon et al. 2017
<i>Microcerotermes serrula</i>	Termitidae	Oriental	KY224710.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp.	Termitidae	Neotropic	KY224722.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp.	Termitidae	Neotropic	KY224534.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp.	Termitidae	Neotropic	KY224585.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp.	Termitidae	Australia	KY224623.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. 1	Termitidae	Oriental	KY224717.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. 3	Termitidae	Oriental	KY224514.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. A	Termitidae	Oriental	KY224612.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. B	Termitidae	Oriental	KY224501.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. C	Termitidae	Australia	KY224430.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. E	Termitidae	Australia	KY224573.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. F	Termitidae	Australia	KY224512.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. G	Termitidae	Australia	KY224635.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. H	Termitidae	Australia	KY224675.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. I	Termitidae	Australia	KY224705.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. SA	Termitidae	Neotropic	KY224435.1	Bourguignon et al. 2017
<i>Microcerotermes</i> sp. SB	Termitidae	Neotropic	KY224578.1	Bourguignon et al. 2017
<i>Microhodotermes viator</i>	Hodotermitidae	Afrotropic	JX144931.1	Cameron et al. 2012
<i>Microtermes mariae</i>	Termitidae	Afrotropic		
<i>Microtermes obesi</i>	Termitidae	Oriental	KY224504.1	Bourguignon et al. 2017
<i>Microtermes obesi</i>	Termitidae	Oriental	KY224524.1	Bourguignon et al. 2017

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<i>Microtermes obesi</i>	Termitidae	Oriental	KY224632.1	Bourguignon et al. 2017
<i>Microtermes</i> sp	Termitidae	Afrotropic		
<i>Microtermes</i> sp.	Termitidae	Afrotropic	KY224416.1	Bourguignon et al. 2017
<i>Microtermes</i> sp.	Termitidae	Afrotropic	KY224511.1	Bourguignon et al. 2017
<i>Microtermes</i> sp.	Termitidae	Afrotropic	KY224539.1	Bourguignon et al. 2017
<i>Microtermes</i> sp.	Termitidae	Afrotropic	KY224545.1	Bourguignon et al. 2017
<i>Microtermes</i> sp.	Termitidae	Oriental	KY224625.1	Bourguignon et al. 2017
<i>Microtermes</i> sp.	Termitidae	Afrotropic	KY224711.1	Bourguignon et al. 2017
<i>Microtermes</i> sp.	Termitidae	Afrotropic	KY224682.1	Bourguignon et al. 2017
<i>Microtermes</i> sp. 1	Termitidae	Oriental	KY224673.1	Bourguignon et al. 2017
<i>Microtermes</i> sp. A	Termitidae	Afrotropic	KY224684.1	Bourguignon et al. 2017
<i>Microtermes</i> sp. B	Termitidae	Afrotropic	KY224615.1	Bourguignon et al. 2017
<i>Microtermes</i> sp. BDIT020	Termitidae	Afrotropic	KY224667.1	Bourguignon et al. 2017
<i>Microtermes</i> sp. C	Termitidae	Oriental	KY224390.1	Bourguignon et al. 2017
<i>Mimeutermes giffardii</i>	Termitidae	Afrotropic		
<i>Mimeutermes sorex</i>	Termitidae	Afrotropic		
<i>Mirocapritermes connectens</i>	Termitidae	Oriental	KY224537.1	Bourguignon et al. 2017
<i>Mirocapritermes</i> sp. 1	Termitidae	Oriental	KY224731.1	Bourguignon et al. 2017
<i>Mirocapritermes</i> sp. 2	Termitidae	Oriental	KY224587.1	Bourguignon et al. 2017
<i>Nasutitermes arborum</i>	Termitidae	Afrotropic	KY224603.1	Bourguignon et al. 2017
<i>Nasutitermes banksi</i>	Termitidae	Neotropic	KY224405.1	Bourguignon et al. 2017
<i>Nasutitermes bikpelanus</i>	Termitidae	Oceanic	KP026296.1	Bourguignon et al. 2015
<i>Nasutitermes diabolus</i>	Termitidae	Afrotropic	KY224393.1	Bourguignon et al. 2017
<i>Nasutitermes exitiosus</i>	Termitidae	Australia	KY224624.1	Bourguignon et al. 2017
<i>Nasutitermes exitiosus</i>	Termitidae	Australia	KY224642.1	Bourguignon et al. 2017
<i>Nasutitermes graveolus</i>	Termitidae	Australia	KY224439.1	Bourguignon et al. 2017
<i>Nasutitermes latifrons</i>	Termitidae	Afrotropic	KY224631.1	Bourguignon et al. 2017
<i>Nasutitermes longinasus</i>	Termitidae	Oriental	KY224407.1	Bourguignon et al. 2017
<i>Nasutitermes longipennis</i>	Termitidae	Australia	KY224483.1	Bourguignon et al. 2017
<i>Nasutitermes longirostris</i>	Termitidae	Oriental	KY224397.1	Bourguignon et al. 2017
<i>Nasutitermes longirostris</i>	Termitidae	Oriental	KY224535.1	Bourguignon et al. 2017
<i>Nasutitermes longirostris</i>	Termitidae	Oriental	KY224677.1	Bourguignon et al. 2017
<i>Nasutitermes lujae</i>	Termitidae	Afrotropic	KY224441.1	Bourguignon et al. 2017
<i>Nasutitermes macrocephalus</i>	Termitidae	Neotropic	KY224724.1	Bourguignon et al. 2017
<i>Nasutitermes matangensis</i>	Termitidae	Oriental	KY224422.1	Bourguignon et al. 2017
<i>Nasutitermes matangensis</i>	Termitidae	Oriental	KY224423.1	Bourguignon et al. 2017
<i>Nasutitermes matangensis</i>	Termitidae	Oriental	KY224561.1	Bourguignon et al. 2017

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<i>Nasutitermes matangensis</i>	Termitidae	Oriental	KY224599.1	Bourguignon et al. 2017
<i>Nasutitermes matangensis</i>	Termitidae	Oriental	KY224639.1	Bourguignon et al. 2017
<i>Nasutitermes matangensis</i>	Termitidae	Oriental	KY224715.1	Bourguignon et al. 2017
<i>Nasutitermes matangensis</i>	Termitidae	Oriental	KY224730.1	Bourguignon et al. 2017
<i>Nasutitermes neoparvus</i>	Termitidae	Oriental	KY224526.1	Bourguignon et al. 2017
<i>Nasutitermes nr. perparvus</i>	Termitidae	Oriental	KP026261.1	Bourguignon et al. 2015
<i>Nasutitermes octopilis</i>	Termitidae	Neotropic	KY224447.1	Bourguignon et al. 2017
<i>Nasutitermes similis</i>	Termitidae	Neotropic	KY224557.1	Bourguignon et al. 2017
<i>Nasutitermes similis</i>	Termitidae	Neotropic	KY238295.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp.	Termitidae	Neotropic	KY224438.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp.	Termitidae	Neotropic	KY224489.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp.	Termitidae	Neotropic	KY224500.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp.	Termitidae	Neotropic	KY224678.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp.	Termitidae	Australia	KY224713.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp. 1	Termitidae	Oriental	KY224707.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp. 2	Termitidae	Oriental	KY224576.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp. 3	Termitidae	Oriental	KY224571.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp. 4	Termitidae	Oriental	KY224664.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp. A	Termitidae	Afrotropic	KY224431.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp. B	Termitidae	Oriental	KY224666.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp. C	Termitidae	Oriental	KY224628.1	Bourguignon et al. 2017
<i>Nasutitermes</i> sp. SC	Termitidae	Neotropic	KY224704.1	Bourguignon et al. 2017
<i>Nasutitermes takasagoensis</i>	Termitidae	Oriental	KP026260.1	Bourguignon et al. 2015
<i>Nasutitermes triodiae</i>	Termitidae	Australia	JX144940.1	Cameron et al. 2012
<i>Nasutitermes triodiae</i>	Termitidae	Australia	KY224403.1	Bourguignon et al. 2017
<i>Neocapritermes angusticeps</i>	Termitidae	Neotropic	KY224467.1	Bourguignon et al. 2017
<i>Neocapritermes araguaia</i>	Termitidae	Neotropic	KP026286.1	Bourguignon et al. 2015
<i>Neocapritermes</i> sp. H	Termitidae	Neotropic	KY224444.1	Bourguignon et al. 2017
<i>Neocapritermes taracua</i>	Termitidae	Neotropic	KY224527.1	Bourguignon et al. 2017
<i>Neotermes insularis</i>	Kalotermitidae	Australia	JX144933.1	Cameron et al. 2012
<i>Neotermes</i> sp. A	Kalotermitidae	Oriental	KP026299.1	Bourguignon et al. 2015
<i>Nitiditermes fulvus</i>	Termitidae	Afrotropic	KY224600.1	Bourguignon et al. 2017
<i>Noditermes cristifrons</i>	Termitidae	Afrotropic	KY224718.1	Bourguignon et al. 2017
<i>Noditermes lamanianus</i>	Termitidae	Afrotropic	KY238294.1	Bourguignon et al. 2017
<i>Occasitermes occasus</i>	Termitidae	Australia	KY224546.1	Bourguignon et al. 2017
<i>Odontotermes formosanus</i>	Termitidae	Oriental	KP026254.1	Bourguignon et al. 2015
<i>Odontotermes hainanensis</i>	Termitidae	Oriental	KY224409.1	Bourguignon et al. 2017

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<i>Odontotermes javanicus</i>	Termitidae	Oriental	KY224596.1	Bourguignon et al. 2017
<i>Odontotermes longignathus</i>	Termitidae	Oriental	KY224665.1	Bourguignon et al. 2017
<i>Odontotermes mathuri</i>	Termitidae	Oriental	KY224427.1	Bourguignon et al. 2017
<i>Odontotermes minutus</i>	Termitidae	Oriental	KY224486.1	Bourguignon et al. 2017
<i>Odontotermes nr. pauperans</i>	Termitidae	Afrotropic	KY224609.1	Bourguignon et al. 2017
<i>Odontotermes obesus</i>	Termitidae	Oriental	KY224406.1	Bourguignon et al. 2017
<i>Odontotermes obesus</i>	Termitidae	Oriental	KY224493.1	Bourguignon et al. 2017
<i>Odontotermes obesus</i>	Termitidae	Oriental	KY238293.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp.	Termitidae	Afrotropic	KY224402.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp.	Termitidae	Afrotropic	KY224446.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp.	Termitidae	Afrotropic	KY224458.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp.	Termitidae	Afrotropic	KY224721.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. 10	Termitidae	Oriental	KY224633.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. 6	Termitidae	Oriental	KY224709.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. 7	Termitidae	Oriental	KY224604.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. A	Termitidae	Oriental	KY224408.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. B	Termitidae	Oriental	KY224551.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. C	Termitidae	Oriental	KY224723.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. D	Termitidae	Afrotropic	KY224520.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. E	Termitidae	Oriental	KY224643.1	Bourguignon et al. 2017
<i>Odontotermes</i> sp. K	Termitidae	Oriental	KY224543.1	Bourguignon et al. 2017
<i>Ophiotermes grandilabius</i>	Termitidae	Afrotropic	KY224515.1	Bourguignon et al. 2017
<i>Ophiotermes mirandus</i>	Termitidae	Afrotropic	KY224495.1	Bourguignon et al. 2017
<i>Oriensubulitermes inanis</i>	Termitidae	Oriental	KY224542.1	Bourguignon et al. 2017
<i>Oriensubulitermes inanis</i>	Termitidae	Oriental	KY224686.1	Bourguignon et al. 2017
<i>Oriensubulitermes inanis</i>	Termitidae	Oriental	KY224692.1	Bourguignon et al. 2017
<i>Orientotermes emersoni</i>	Termitidae	Oriental	KY224456.1	Bourguignon et al. 2017
<i>Orthognathotermes aduncus</i>	Termitidae	Neotropic	KP026289.1	Bourguignon et al. 2015
<i>Orthotermes depressifrons</i>	Termitidae	Afrotropic	KY224654.1	Bourguignon et al. 2017
<i>Orthotermes mansuetus</i>	Termitidae	Afrotropic	KY224579.1	Bourguignon et al. 2017
<i>Palmitermes impostor</i>	Termitidae	Neotropic	KY224567.1	Bourguignon et al. 2017
<i>Palmitermes impostor</i>	Termitidae	Neotropic	KY224697.1	Bourguignon et al. 2017
<i>Parrhinotermes aequalis</i>	Rhinotermitidae	Oriental	MK246849.1	Wang et al. 2019
<i>Parrhinotermes browni</i>	Rhinotermitidae	Oceanic	KP026295.1	Bourguignon et al. 2015
<i>Parrhinotermes microdentiformis</i>	Rhinotermitidae	Oriental	MK246851.1	Wang et al. 2019
<i>Parrhinotermes</i> sp. A	Rhinotermitidae	Oriental	MK246854.1	Wang et al. 2019
<i>Parrhinotermes</i> sp. B	Rhinotermitidae	Oriental	MK246848.1	Wang et al. 2019

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<i>Parrhinotermes</i> sp. C	Rhinotermitidae	Oriental	MK2246842.1	Wang et al. 2019
<i>Patawatermes nigripunctatus</i>	Termitidae	Neotropic	KY224420.1	Bourguignon et al. 2017
<i>Patawatermes nigripunctatus</i>	Termitidae	Neotropic	KY224476.1	Bourguignon et al. 2017
<i>Patawatermes</i> sp. A	Termitidae	Neotropic	KY224396.1	Bourguignon et al. 2017
<i>Patawatermes turricola</i>	Termitidae	Neotropic	KY224693.1	Bourguignon et al. 2017
<i>Pericapritermes dolichocephalus</i>	Termitidae	Oriental	KY224616.1	Bourguignon et al. 2017
<i>Pericapritermes dolichocephalus</i>	Termitidae	Oriental	KY224648.1	Bourguignon et al. 2017
<i>Pericapritermes latignathus</i>	Termitidae	Oriental	KY224425.1	Bourguignon et al. 2017
<i>Pericapritermes nigerianus</i>	Termitidae	Afrotropic	KP026278.1	Bourguignon et al. 2015
<i>Pericapritermes nitobei</i>	Termitidae	Oriental	KY224470.1	Bourguignon et al. 2017
<i>Pericapritermes</i> sp.	Termitidae	Oriental	KY224608.1	Bourguignon et al. 2017
<i>Pericapritermes</i> sp. 2	Termitidae	Oriental	KY224398.1	Bourguignon et al. 2017
<i>Pericapritermes</i> sp. 3	Termitidae	Oriental	KY224681.1	Bourguignon et al. 2017
<i>Pericapritermes</i> sp. 4	Termitidae	Oriental	KY224454.1	Bourguignon et al. 2017
<i>Pericapritermes</i> sp. A	Termitidae	Afrotropic	KY224589.1	Bourguignon et al. 2017
<i>Pericapritermes</i> sp. B	Termitidae	Afrotropic	KY224618.1	Bourguignon et al. 2017
<i>Pericapritermes</i> sp. G	Termitidae	Oriental	KY224519.1	Bourguignon et al. 2017
<i>Planicapritermes planiceps</i>	Termitidae	Neotropic	KY224552.1	Bourguignon et al. 2017
<i>Polyspathotermes bugeserae</i>	Termitidae	Afrotropic	KY224421.1	Bourguignon et al. 2017
<i>Polyspathotermes</i> sp. aff. <i>katangensis</i>	Termitidae	Afrotropic	KY224475.1	Bourguignon et al. 2017
<i>Polyspathotermes sulcifrons</i>	Termitidae	Afrotropic	KY224606.1	Bourguignon et al. 2017
<i>Porotermes adamsoni</i>	Stolotermitidae	Australia	JX144930.1	Cameron et al. 2012
<i>Postsubulitermes parviconstrictus</i>	Termitidae	Afrotropic	KP026268.1	Bourguignon et al. 2015
<i>Postsubulitermes parviconstrictus</i>	Termitidae	Afrotropic	KY224622.1	Bourguignon et al. 2017
<i>Proboscitermes tubuliferus</i>	Termitidae	Afrotropic	KY224503.1	Bourguignon et al. 2017
<i>Procapritermes martyni</i>	Termitidae	Oriental	KY224638.1	Bourguignon et al. 2017
<i>Procapritermes</i> sp. 1	Termitidae	Oriental	KY224437.1	Bourguignon et al. 2017
<i>Procapritermes</i> sp. A	Termitidae	Oriental	KY224597.1	Bourguignon et al. 2017
<i>Procapritermes</i> sp. C	Termitidae	Oriental	KY224482.1	Bourguignon et al. 2017
<i>Procapritermes</i> sp. G	Termitidae	Oriental	KY224592.1	Bourguignon et al. 2017
<i>Procornitermes araujoi</i>	Termitidae	Neotropic	KY224636.1	Bourguignon et al. 2017
<i>Procubitermes arboricola</i>	Termitidae	Afrotropic	KP026273.1	Bourguignon et al. 2015
<i>Procubitermes undulans</i>	Termitidae	Afrotropic	KY224694.1	Bourguignon et al. 2017
<i>Prohamitermes mirabilis</i>	Termitidae	Oriental	KY224433.1	Bourguignon et al. 2017
<i>Prohamitermes mirabilis</i>	Termitidae	Oriental	KY224617.1	Bourguignon et al. 2017
<i>Promirotermes pygmaeus</i>	Termitidae	Afrotropic	KY224529.1	Bourguignon et al. 2017
<i>Promirotermes redundans</i>	Termitidae	Afrotropic	KP026266.1	Bourguignon et al. 2015

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<i>Promirotermes</i> sp. A	Termitidae	Afrotropic	KY224554.1	Bourguignon et al. 2017
<i>Prorhinotermes canalifrons</i>	Rhinotermitidae	Madagascar	KP026256.1	Bourguignon et al. 2015
<i>Prorhinotermes inopinatus</i>	Rhinotermitidae	Oceanic		
<i>Prorhinotermes molinoi</i>	Rhinotermitidae	Neotropic		ID by RH Scheffrahn
<i>Prorhinotermes simplex</i>	Rhinotermitidae	Neotropic		
<i>Protermes prorepens</i>	Termitidae	Afrotropic	KY224658.1	Bourguignon et al. 2017
<i>Psammotermes</i> sp.	Rhinotermitidae	Saharo_Arabian		
<i>Pseudacanthotermes militaris</i>	Termitidae	Afrotropic	KY224517.1	Bourguignon et al. 2017
<i>Pseudacanthotermes spiniger</i>	Termitidae	Afrotropic	KY224401.1	Bourguignon et al. 2017
<i>Reticulitermes flavipes</i>	Rhinotermitidae	Nearctic	EF206314.1	Cameron and Whiting 2007
<i>Reticulitermes hageni</i>	Rhinotermitidae	Nearctic	EF206320.1	Cameron and Whiting 2007
<i>Reticulitermes santonensis</i>	Rhinotermitidae	Palaeartic	EF206315.1	Cameron and Whiting 2007
<i>Reticulitermes virginicus</i>	Rhinotermitidae	Nearctic	EF206319.1	Cameron and Whiting 2007
<i>Rhinotermes hispidus</i>	Rhinotermitidae	Neotropic	KU925240.1	Bourguignon et al. 2016
<i>Rhynchotermes nasutissimus</i>	Termitidae	Neotropic	KY224701.1	Bourguignon et al. 2017
<i>Rubeotermes jheringi</i>	Termitidae	Neotropic	KY224614.1	Bourguignon et al. 2017
<i>Rugitermes</i> sp. A	Kalotermitidae	Neotropic	KP026284.1	Bourguignon et al. 2015
<i>Ruptitermes arboreus</i>	Termitidae	Neotropic	KY224706.1	Bourguignon et al. 2017
<i>Ruptitermes</i> nr. <i>xanthochiton</i>	Termitidae	Neotropic	KY224594.1	Bourguignon et al. 2017
<i>Schedorhinotermes breinli</i>	Rhinotermitidae	Australia	JX144935.1	Cameron et al. 2012
<i>Schedorhinotermes breinli</i>	Rhinotermitidae	Australia	MK246841.1	Wang et al. 2019
<i>Schedorhinotermes lamanianus</i>	Rhinotermitidae	Afrotropic	MK246844.1	Wang et al. 2019
<i>Schedorhinotermes longirostris</i>	Rhinotermitidae	Oriental	MK246846.1	Wang et al. 2019
<i>Schedorhinotermes medioobscurus</i>	Rhinotermitidae	Oriental	MK246845.1	Wang et al. 2019
<i>Schedorhinotermes putorius</i>	Rhinotermitidae	Afrotropic	MK246843.1	Wang et al. 2019
<i>Schedorhinotermes sarawakensis</i>	Rhinotermitidae	Oriental	MK246852.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp.	Rhinotermitidae	Oriental	MK246857.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 1	Rhinotermitidae	Oriental	MK246855.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 10	Rhinotermitidae	Oriental	MK246859.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 3	Rhinotermitidae	Oriental	MK246856.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 4	Rhinotermitidae	Australia	MK246837.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 5	Rhinotermitidae	Oriental	MK246850.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 6	Rhinotermitidae	Australia	MK246838.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 7	Rhinotermitidae	Australia	MK246839.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 8	Rhinotermitidae	Australia	MK246840.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp. 9	Rhinotermitidae	Oriental	MK246853.1	Wang et al. 2019
<i>Schedorhinotermes</i> sp.2	Rhinotermitidae	Oriental	MK246858.1	Wang et al. 2019

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<i>Schedorhinotermes translucens</i>	Rhinotermitidae	Oriental	MK246847.1	Wang et al. 2019
<i>Serritermes serrifer</i>	Serritermitidae	Neotropic	KP026264.1	Bourguignon et al. 2015
<i>Silvestritermes heyeri</i>	Termitidae	Neotropic	KY224492.1	Bourguignon et al. 2017
<i>Silvestritermes heyeri</i>	Termitidae	Neotropic	KY224619.1	Bourguignon et al. 2017
<i>Silvestritermes holmgreni</i>	Termitidae	Neotropic	KP026288.1	Bourguignon et al. 2015
<i>Sinocapritermes mushae</i>	Termitidae	Oriental	KP026255.1	Bourguignon et al. 2015
<i>Sinocapritermes</i> sp. 1	Termitidae	Oriental	KY224541.1	Bourguignon et al. 2017
<i>Sphaerotermes</i> sp. A	Termitidae	Afrotropic	KY238292.1	Bourguignon et al. 2017
<i>Sphaerotermes sphaerothorax</i>	Termitidae	Afrotropic	KP026279.1	Bourguignon et al. 2015
<i>Sphaerotermes sphaerothorax</i>	Termitidae	Afrotropic	KY224584.1	Bourguignon et al. 2017
<i>Spinitermes longiceps</i>	Termitidae	Neotropic	KY224637.1	Bourguignon et al. 2017
<i>Spinitermes</i> sp. A	Termitidae	Neotropic	KY224550.1	Bourguignon et al. 2017
<i>Spinitermes trispinosus</i>	Termitidae	Neotropic	KY224553.1	Bourguignon et al. 2017
<i>Subulitermes</i> group sp. A	Termitidae	Neotropic	KY224414.1	Bourguignon et al. 2017
<i>Subulitermes</i> sp.	Termitidae	Neotropic	KY224562.1	Bourguignon et al. 2017
<i>Synacanthotermes</i> sp.	Termitidae	Afrotropic	KP026270.1	Bourguignon et al. 2015
<i>Syntermes spinosus</i>	Termitidae	Neotropic	KP026293.1	Bourguignon et al. 2015
<i>Termes comis</i>	Termitidae	Oriental	KY224644.1	Bourguignon et al. 2017
<i>Termes fatalis</i>	Termitidae	Neotropic	KY224457.1	Bourguignon et al. 2017
<i>Termes fatalis</i>	Termitidae	Neotropic	KY224507.1	Bourguignon et al. 2017
<i>Termes fatalis</i>	Termitidae	Neotropic	KY224572.1	Bourguignon et al. 2017
<i>Termes fatalis</i>	Termitidae	Neotropic	KY224726.1	Bourguignon et al. 2017
<i>Termes</i> group sp. F	Termitidae	Australia	KY224560.1	Bourguignon et al. 2017
<i>Termes hospes</i>	Termitidae	Afrotropic	KY224412.1	Bourguignon et al. 2017
<i>Termes hospes</i>	Termitidae	Afrotropic	KY224510.1	Bourguignon et al. 2017
<i>Termes rostratus</i>	Termitidae	Oriental	KY224442.1	Bourguignon et al. 2017
<i>Termes rostratus</i>	Termitidae	Oriental	KY224453.1	Bourguignon et al. 2017
<i>Termes rostratus</i>	Termitidae	Oriental	KY224595.1	Bourguignon et al. 2017
<i>Termitogeton planus</i>	Rhinotermitidae	Oceanic	KP026298.1	Bourguignon et al. 2015
<i>Tetimatermes</i> sp. A	Termitidae	Neotropic	KY224655.1	Bourguignon et al. 2017
<i>Thoracotermes macrothorax</i>	Termitidae	Afrotropic	KY224714.1	Bourguignon et al. 2017
<i>Trichotermes ducis</i>	Termitidae	Afrotropic	KY224506.1	Bourguignon et al. 2017
<i>Trinervitermes geminatus</i>	Termitidae	Afrotropic		
<i>Trinervitermes gratiosus</i>	Termitidae	Afrotropic		
<i>Trinervitermes</i> sp.	Termitidae	Oriental	KY224626.1	Bourguignon et al. 2017
<i>Trinervitermes</i> sp. A	Termitidae	Afrotropic	KY224523.1	Bourguignon et al. 2017
<i>Tuberculitermes bycanistes</i>	Termitidae	Neotropic	KY224466.1	Bourguignon et al. 2017

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<i>Tumulitermes pastinator</i>	Termitidae	Australia	KY224570.1	Bourguignon et al. 2017
<i>Tumulitermes recalvus</i>	Termitidae	Australia	KY224463.1	Bourguignon et al. 2017
<i>Tumulitermes</i> sp.	Termitidae	Australia	KY224647.1	Bourguignon et al. 2017
<i>Tumulitermes</i> sp.	Termitidae	Australia	KY224696.1	Bourguignon et al. 2017
Unidentified Cubitermitinae	Termitidae	Afrotropic		ID by RH Scheffrahn
unidentified Nasutitermitinae	Termitidae	Nearctic		ID by RH Scheffrahn
<i>Zootermopsis angusticollis</i>	Archotermopsidae	Nearctic	JX144932.1	Cameron et al. 2012

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Table S3. 2 Fossils used for time calibrations in this study.

Fossil species	Minimum age constraint (MY)	Calibration group	Soft maximum bound (97.5% probability)	Reference	Note on maximum bound
<i>Melqartitermes myrreus</i>	125.45	Mastotermitidae + sister group	235	Engel et al. 2007	<i>Triassoblatta argentina</i> , earliest fossil of Mesoblattinidae (Martins-Neto et al. 2005)
<i>Cosmotermes multus</i>	94.3	Stolotermitidae + Hodotermitidae + Archotermopsidae	235	Zhao et al. 2020	<i>Triassoblatta argentina</i> , earliest fossil of Mesoblattinidae (Martins-Neto et al. 2005)
<i>Archeorhinotermes rossi</i>	94.3	Neoisoptera	235	Krishna and Grimaldi 2003	<i>Triassoblatta argentina</i> , earliest fossil of Mesoblattinidae (Martins-Neto et al. 2005)
<i>Nanotermes isaacae</i>	47.8	Termitidae + <i>Coptotermes</i> + <i>Heterotermes</i> + <i>Reticulitermes</i>	94.3	Engel et al. 2011	First fossil of Rhinotermitinae
<i>Reticulitermes antiquus</i>	33.9	<i>Reticulitermes</i> + <i>Coptotermes</i> + <i>Heterotermes</i>	94.3	Engel et al. 2007b	First fossil of Rhinotermitinae
<i>Dolichorhinotermes dominicanus</i>	16	<i>Dolichorhinotermes</i> + <i>Rhinotermes</i>	94.3	Schlemmermeyer and Canello 2000	First fossil of Rhinotermitinae
<i>Coptotermes sucineus</i>	16	<i>Coptotermes</i> + sister <i>Heterotermes</i> lineage	33.9	Emerson 1971	First <i>Heterotermes</i> fossil
<i>Macrotermes pristinus</i>	16	<i>Macrotermes</i> + sister group	47.8	Charpentier 1843	First fossil of Termitidae
<i>Constrictotermes electroconstrictus</i>	13.8	<i>Constrictotermes</i> + sister group	47.8	Krishna 1996	First fossil of Termitidae
<i>Anoplotermes sensu lato</i>	13.8	South American <i>Anoplotermes</i> -group + <i>Euhamitermes</i>	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae
<i>Microcerotermes insularis</i>	13.8	<i>Microcerotermes</i> + Syntermitinae	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae
<i>Amitermes lucidus</i>	13.8	<i>Amitermes</i> + <i>Drepanotermes</i> + <i>Gnathamitermes</i> + <i>Orthognathotermes</i>	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae
<i>Termes primitivus</i>	13.8	<i>Tuberculitermes</i> + <i>Dihoplotermes</i> + <i>Spinitermes</i> + <i>Palmitermes</i> + <i>Termes</i> + <i>Cavitermes</i> + <i>Inquilinitermes</i> + <i>Quasitermes</i> + <i>Capritermes</i> + <i>Ephelotermes</i> + <i>Macrogathotermes</i> + <i>Lophotermes</i>	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae
<i>Atlantitermes antillea</i>	13.8	<i>Subulitermes</i> + <i>Araujotermes</i> + <i>Atlantitermes</i> + <i>Coatitermes</i> + <i>Agnathotermes</i> + sister group	47.8	Krishna and Grimaldi 2009	First fossil of Termitidae

## Appendices

Table S3. 3 Statistical comparisons of DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE and BAYAREALIKE+J for the six phylogenetic trees reconstructed in this study.

Likelihood Ratio Tests (LRT) were performed to determine the effect of jumping speciation events for each pair of models. Models were statistically compared using corrected Aikake Information Criterion (AICc) weights. Abbreviations: d, dispersal rate between biogeographic realms; e, local extinction rate.

	model	LnL	num para ms	d	e	j	AICc	AICc_wt	p- val(LRT)
IQ-TREE (with the third codon position excluded)	DEC	-518.4	2	0.21	0.21	0	1041	1.50E-53	5.20E-55
	DEC+J	-396.4	3	1.00E-12	1.00E-12	0.0091	798.8	0.55	
	DIVALIKE	-498.5	2	0.24	0.026	0	1001	6.80E-45	
	DIVALIKE+J	-396.7	3	1.00E-12	1.00E-12	0.0086	799.4	0.41	
	BAYAREALIKE	-679.1	2	0.24	2.83	0	1362	2.40E-123	
BAYAREALIKE+J	-399.1	3	1.00E-07	1.00E-07	0.0087	804.3	0.035		
IQ-TREE (with the third codon position)	DEC	-515.8	2	0.17	0.16	0	1036	6.40E-53	2.00E-54
	DEC+J	-395.2	3	1.00E-12	1.00E-12	0.0085	796.4	0.59	
	DIVALIKE	-494.3	2	0.2	0.0045	0	992.7	1.40E-43	
	DIVALIKE+J	-395.6	3	1.00E-12	1.00E-12	0.0086	797.3	0.38	
	BAYAREALIKE	-679.1	2	0.19	2.4	0	1362	8.00E-124	
BAYAREALIKE+J	-398.1	3	1.00E-07	1.00E-07	0.0087	802.2	0.032		
MrBayes Tree (with the third codon position excluded)	DEC	-510.9	2	0.25	0.2	0	1026	2.20E-50	6.20E-48
	DEC+J	-405.2	3	1.00E-12	0.32	0.0087	816.4	7.00E-05	
	DIVALIKE	-485.5	2	0.29	1.00E-12	0	975.1	2.40E-39	
	DIVALIKE+J	-395.7	3	1.00E-12	1.00E-12	0.0086	797.5	0.88	
	BAYAREALIKE	-670.6	2	0.3	3.61	0	1345	1.00E-119	
BAYAREALIKE+J	-397.7	3	1.00E-07	1.00E-07	0.0086	801.4	0.12		
MrBayes Tree (with the third codon position)	DEC	-511.9	2	0.15	0.13	0	1028	1.90E-51	5.60E-53
	DEC+J	-394.5	3	1.00E-12	2.90E-08	0.0085	795	0.65	
	DIVALIKE	-487.8	2	0.17	1.00E-12	0	979.7	5.30E-41	
	DIVALIKE+J	-395.3	3	1.00E-12	1.00E-12	0.0086	796.6	0.31	
	BAYAREALIKE	-675	2	0.16	2.02	0	1354	2.70E-122	
BAYAREALIKE+J	-397.2	3	1.00E-07	1.00E-07	0.0086	800.5	0.043		
BEAST Tree (with the third codon position excluded)	DEC	-506.8	2	0.0014	0.0013	0	1018	2.90E-49	1.30E-50
	DEC+J	-394.9	3	1.00E-12	2.90E-10	0.0085	795.8	0.44	
	DIVALIKE	-479.4	2	0.0016	1.00E-12	0	962.8	2.40E-37	
	DIVALIKE+J	-394.7	3	1.00E-12	1.00E-12	0.0085	795.4	0.53	
	BAYAREALIKE	-873.6	2	0.01	0.01	0	1751	1.50E-208	
BAYAREALIKE+J	-397.8	3	1.00E-07	1.00E-07	0.0086	801.6	0.024		
	DEC	-765.3	2	0.01	0.01	0	1535	8.50E-162	1.40E-163

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BEAST Tree (with the third codon position)	DEC+J	-393.8	3	1.00E- 12	1.00E- 12	0.00 85	793. 7	0.65	
	DIVALIKE	-484.2	2	0.0015	1.00E- 12	0	972. 5	9.50E-40	6.70E-41
	DIVALIKE+J	-394.6	3	1.00E- 12	1.00E- 12	0.00 86	795. 2	0.31	
	BAYAREALI KE	-907.6	2	0.01	0.01	0	181 9	1.40E-223	2.90E- 224
	BAYAREALI KE+J	-396.5	3	1.00E- 07	1.00E- 07	0.00 86	799. 1	0.043	