

Rapid Communication**First record of three alien termite species in Belgium**

Ann Vanderheyden¹, Wouter Dekoninck¹, Nathalie Smitz², Anicée Lombal¹, Marc De Meyer²
and Thierry Backeljau^{1,3}

¹Royal Belgian Institute of Natural Sciences (BopCo & Scientific Heritage Service), Vautierstraat 29, 1000 Brussels, Belgium

²Royal Museum for Central Africa (BopCo & Biology Department), Leuvensesteenweg 13, 3080 Tervuren, Belgium

³Evolutionary Ecology Group, University of Antwerp, Universiteitsplein 1, 2610 Antwerp, Belgium

Corresponding author: Ann Vanderheyden (avanderheyden@naturalsciences.be)

Citation: Vanderheyden A, Dekoninck W, Smitz N, Lombal A, Meyer D, Backeljau T (2024) First record of three alien termite species in Belgium. *BioInvasions Records* 13(2): 335–344, <https://doi.org/10.3391/bir.2024.13.2.04>

Received: 25 October 2023

Accepted: 9 February 2024

Published: 21 April 2024

Handling editor: Ben Hoffmann

Thematic editor: Stelios Katsanevakis

Copyright: © Vanderheyden et al.

This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International - CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

OPEN ACCESS

Abstract

Subterranean termites (Family Rhinotermitidae) and drywood termites (Family Kalotermitidae) can be pest species as they have the potential to inflict damage to wooden constructions and can therefore cause a significant economic impact. Some species of these families are highly destructive and are invasive in many parts of the world. New introductions and/or the spread of termites are often caused by import of infested wood, plants or soils. The present study reports the first records of three exotic termite species in Belgium, viz. *Cryptotermes brevis* and *Reticulitermes banyulensis* in Brussels (Brussels Capital Region), and *Reticulitermes flavipes* in Brugelette (Hainaut province; Walloon region). The morphological identification of the specimens (N = 8) was validated by DNA-barcoding. *Cryptotermes brevis* and *Reticulitermes banyulensis* infestations are probably of little concern as local climatological conditions make it unlikely for either species to survive in the temperate climate in Belgium. In contrast, it is likely that *Reticulitermes flavipes* may become established and will spread to other sites in Belgium.

Key words: Invasive termites, *Cryptotermes brevis*, *Reticulitermes banyulensis*, *Reticulitermes flavipes*, DNA-barcoding, cytochrome c oxidase subunit I, cytochrome c oxidase subunit II

Introduction

Termites can be pest species because their feeding habits may damage agricultural crops, timber in buildings, post fences, earth dams, and irrigation canals (Gay 1967; Su and Scheffrahn 2000). Drywood termites (Family Kalotermitidae) and subterranean termites (Family Rhinotermitidae) are major urban pests as they have the potential to inflict damage to man-made wood constructions, including almost any type of wood (Scheffrahn and Su 2014). However, some termite species need specific climatological conditions to survive, so that their dispersal capacity is limited by temperature and humidity constraints of their native environments (Emerson 1936; Kutnik et al. 2004; Scheffrahn et al. 2009).

Amongst drywood termites, *Cryptotermes brevis* (Walker, 1853), the West Indian drywood termite, is invasive and highly destructive in several parts of the world. The species was originally described from infestations in

Jamaica. Its natural habitat remained unknown until 2007 when small colonies were discovered in natural drywood in the desert in Chile and coastal Peru (Scheffrahn et al. 2009). *Cryptotermes brevis* is therefore considered to be native to south America. The specific desert climate conditions in the native area of *C. brevis* (stable and humid) may have allowed the species to survive and hitchhike in lumber and wooden artifacts transported around the world, and so to infest new territories (Scheffrahn et al. 2009). However, the establishment and spread of *C. brevis* in Europe is restricted to sheltered wood and man-made lumber structures within certain environmental and climatic conditions (Rust and Cabrera 1994), since *C. brevis* can only flourish under strict humidity and temperature levels (1.44–2.2 temperature dew point ratio) (Scheffrahn et al. 2009). In Europe, *C. brevis* has been introduced via wood trade in Germany (Becker and Kny 1977), Italy (Raineri et al. 2001; Fontana and Buzetti 2003; Liotta 2005), Spain and Portugal (Nunes et al. 2010), and the United Kingdom (Gay 1967). The most destructive *C. brevis* infestations in Europe occur in the Azores, where many buildings with timber floor and roof structures are infested (Nunes et al. 2005). Well established populations have also been found on the Iberian Peninsula (Nunes et al. 2010). Controlling these infestations and repairing the damages are so expensive that the species is considered to have a significant economic impact (Raineri et al. 2001; Nunes et al. 2005).

Subterranean termites of the genus *Reticulitermes* (Rhinotermitidae) also include major invasive species, of which *R. flavipes* (Kollar, 1837) has the widest geographic distribution (Austin et al. 2012). In 1837, it was accidentally introduced in Europe (Vienna; Austria) by importation of infested plants from the USA (Kollar 1837). Since 1924, it is also established in France (reported under the junior synonym *Reticulitermes santonensis*) (Feytaud 1924; Austin et al. 2005; Vargo and Husseneder 2009; Baudouin et al. 2018). *Reticulitermes flavipes* was subsequently recorded in the Canary Islands (Hernández-Teixidor et al. 2019), Germany (Gay 1967; Weidner 1937), Italy (Ghesini et al. 2010) and the Netherlands (de Visser et al. 2023). The species causes damage to man-made structures (mainly old buildings), trees and crops (Ghesini et al. 2010; Hernández-Teixidor et al. 2019). It resists low temperatures (as low as 3.4 °C) and thrives in temperate regions (Cao and Su 2016).

In contrast to *Reticulitermes flavipes*, *R. banyulensis* Clément, 1978 is so far only known from Spain and France (Kutnik et al. 2004). While this species also feeds on, and thus may damage, wooden structures, it is not considered as an invasive species because its populations are too small and its distribution too limited (Clément et al. 2001; Kutnik et al. 2004).

Aside from a mention of *C. brevis* in local news in Arlon (personal communication Philippe Wegnez) up until now there were no documented records of termites in Belgium. Hence, this paper is the first scientific report on the occurrence of *Cryptotermes brevis*, *Reticulitermes flavipes* and *R. banyulensis* in Belgium, with observations of nuptial flights of *C. brevis* in heated buildings and at least one colony of *R. flavipes* developing outside.

Materials and methods

Since 2020 several cases of termite infestation were reported to the Royal Belgian Institute of Natural Sciences (RBINS). In 2020 specimens were collected in the Up-site residential tower at Quai des Péniches, Brussels and in a residential house in the Avenue de Floreal, Uccle. Moreover in a greenhouse in Brugelette (Hainaut province; Walloon region) termites were collected in the summer of 2022. Eight termite specimens were used for DNA extraction, and several voucher specimens from each location were stored in the collection of RBINS (general inventory registration numbers: IG 34433; IG 34636). Prior to DNA extraction, specimens were independently identified morphologically by Yves Roisin (Université Libre de Bruxelles) and one of the authors (WD), using the identification keys of Scheffrahn and Su (1994) and Roisin (2020).

The QIAamp DNA Mini Kit (Qiagen) was used to extract DNA following the manufacturer's protocols. A 658 bp fragment of the cytochrome *c* oxidase subunit I (COI) gene was amplified using LCO1490 (5'-GGTCAA CAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGG TGACCAAAAAATCA-3') primers (Folmer et al. 1994). A 669 bp fragment of the COI gene was amplified using C1F0 (5'-ATTTTGATTCTTTGG TCACC-3') and C1R1 (5'-ATGAATARRAAYATTACTC-3') primers (Lo et al. 2004). Finally, a 749 bp fragment of the cytochrome *c* oxidase subunit II (COII) gene was amplified using the newly designed primer COIIA-tLeumod (5'-TCTATTTTGGCAGATAAGTG-3') (based on the GenBank sequence MW208858 of *Cryptotermes havilandi*) and COIIB-tLys (5'-GTTTAAGAGACCACTACTTG-3') (adapted from Ghesini et al. 2020).

PCR amplifications were performed in a total volume of 25 µl, containing 2 µl of DNA and 0.2 µM of each primer, and using the 2x Qiagen® Multiplex PCR Kit (Qiagen) with HotStarTaq® DNA polymerase. For both gene fragments, the PCR profile was: 15 min at 95 °C followed by 35 cycles of 45 s at 95 °C, 45 s at 53 °C and 60 s at 72 °C, with a final extension step of 10 min at 72 °C. All PCR products were purified using the ExoSAP-IT protocol (ThermoFisher) and were sent for bidirectional sequencing to Macrogen (Amsterdam, the Netherlands). Sequences were trimmed, corrected, translated into amino acids and assembled using Geneious Prime® 2019.2.3 (Biomatters Ltd.). A consensus sequence was generated for each specimen and each gene fragment, and was then compared with sequences in online reference databases using the BLAST tool in Geneious Prime® 2019.2.3.

All publicly available COI and COII sequences from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>, September 2023) and BOLD (<https://www.boldsystems.org/>, September 2023) for the family Kalotermitidae and the subfamily Heterotermitinae of the Rhinotermitidae were downloaded and aligned using ClustalW in Geneious Prime® 2019.2.3 (Biomatters Ltd.). The alignments were then checked for stop codons and trimmed to retain the

Table 1. BLAST results of sequenced specimens.

Field code	Location		BLAST result (Pairwise identity)		
			COI (658 bp)	COI (669 bp)	COII
SW101	Brussels	in apartment	<i>Cryptotermes brevis</i> 96.3%	Not sequenced	<i>Cryptotermes brevis</i> 99.6%
SW102	Brussels	in apartment	<i>Cryptotermes brevis</i> 96.4%	Not sequenced	<i>Cryptotermes brevis</i> 99.5%
SW103	Uccle	in residential house	<i>Reticulitermes grassei</i> 94.9%	<i>Reticulitermes banyulensis</i> 100 %	<i>Reticulitermes grassei/banyulensis</i> 99.4%
SW104	Uccle	in residential house	<i>Reticulitermes grassei</i> 95.3%	<i>Reticulitermes banyulensis</i> 99.7 %	<i>Reticulitermes grassei/banyulensis</i> 99.7%
SW105	Uccle	in residential house	<i>Reticulitermes grassei</i> 95%	<i>Reticulitermes banyulensis</i> 100 %	<i>Reticulitermes grassei/banyulensis</i> 99.6 %
SW106	Uccle	in residential house	<i>Reticulitermes grassei</i> 95%	<i>Reticulitermes banyulensis</i> 100%	<i>Reticulitermes grassei/banyulensis</i> 99.6%
SW107	Brugelette	inside and outside green house	<i>Reticulitermes flavipes</i> 99.1%	<i>Reticulitermes flavipes</i> 98.5%	<i>Reticulitermes flavipes</i> 99.0%
SW108	Brugelette	inside and outside green house	<i>Reticulitermes flavipes</i> 99.1%	<i>Reticulitermes flavipes</i> 98.6%	<i>Reticulitermes flavipes</i> 99.0%

658 bp and 669 bp regions for COI and the 749 bp region for COII. Sequences of less than 300 bp and conspecific identical sequences were discarded. New sequences and downloaded Kalotermitidae and Heterotermitinae sequences were used to construct Neighbor-Joining (NJ) trees in Geneious® v.10.0.4 (Biomatters Ltd.) using the Tamura-Nei distance model. Trees of Kalotermitidae were rooted with sequences of *Mastotermes darwiniensis* Froggatt, 1897 (family Mastotermitidae) (GenBank accession numbers: FJ806882, MT188750) and trees of Heterotermitinae were rooted with sequences of *Globitermes sulphureus* (Haviland, 1898) and *Pericapritermes nitobei* (Shiraki, 1909) (family Termitidae) (GenBank accession numbers: MF997575, OM472586, MW073092, MW073096). Branch support was assessed via nonparametric bootstrapping using 1,000 bootstrap replicates and a 70% cut-off level.

Results

In June 2020 three nuptial termite flights were observed in the Brussels Up-site residential tower. On July 4th 2020, three termite specimens were collected on site and transferred to RBINS for species identification. Nuptial flights were again observed between April 29th and May 9th 2021. In Uccle (Avenue de Floreal) termites were collected in a residential house in the summer of 2022. Finally, on April 27th 2022, termites were collected in two greenhouses in a zoo at Brugelette. Many large nests were discovered inside, as well as in the adjacent bamboo vegetation outside one of the greenhouses.

The morphological species identification was resolved up to the genus level, viz. the genus *Cryptotermes* (Kalotermitidae) for the specimens from the Up-site residential tower in Brussels and the genus *Reticulitermes* (family Heterotermitidae) for the specimens from Uccle and Brugelette.

For the samples collected in the Up-site residential tower in Brussels the BLAST results yielded a best matching pairwise sequence identity of 96.3% for COI (658 bp) and of 99.6% for COII with *Cryptotermes brevis* (Table 1). Moreover, the new COII sequences cluster with maximum support (100%) with other *Cryptotermes brevis* sequences in the NJ-tree (Figure 1). For the



Figure 1. NJ-tree of COII sequences of the family Kalotermitidae, using *Mastotermes darwiniensis* (family Mastotermitidae) as outgroup (Tamura-Nei distance model, 1,000 bootstrap replicates, 70% cut off threshold). Bootstrap values are indicated at the branch nodes. Sequences were collapsed in species-clusters for readability. New sequences are indicated in red.

specimens from Uccle, the COI (669 bp region) and COII BLAST results matched the new COI and COII sequences to *Reticulitermes grassei* or *Reticulitermes banyulensis* with a 99.4%–100% pairwise sequence identity (Table 1). The new COI (669 bp region) and COII sequences from Brugelette, using BLAST, were recovered with 98.5–99% similarities to *Reticulitermes flavipes* (Table 1). In the NJ-tree, the new COI sequences (669 bp region) cluster with maximum support with other sequences of *Reticulitermes banyulensis* (100%) and *Reticulitermes flavipes* (92%), respectively (Figure 2). The new sequences were deposited in GenBank (COI: OR661722–OR661735 ; COII: OR669088–OR669095).

Discussion

Globalization, trade of goods and other anthropogenic factors are at the root of the worldwide distribution of eusocial insects (including termites) (Bertelsmeier 2021). According to Evans (2021) six invasive termite species with significant economic impact are known to spread extensively from their native habitat to urban or other non-native habitats worldwide. Three of these invasive termite species have reached Europe, viz. *Reticulitermes flavipes*, *Coptotermes gestroi* (Wasmann, 1896) and *Cryptotermes brevis* (Ghesini et al. 2011; Borges et al. 2014; Hernández-Teixidor et al. 2019). Infested commercial shipping and infested cargo probably distributed *C. brevis* and *R. flavipes* termites between ports as early as the 17th century (Feytaud 1924; Bagnères et al. 1990; Clément et al. 2001; Scheffrahn et al. 2009; Perdereau et al. 2013).

It is unclear how *Cryptotermes brevis* and *Reticulitermes banyulensis* arrived in Brussels or when the infestations started. Based on similar cases in England (Gay 1967) and Germany (Becker and Kny 1977), it is assumed that *C. brevis* may have been transported in wooden artifacts by inhabitants of the apartment complex. The microclimates in buildings may allow *C. brevis* colonies to develop in temperate regions, however outdoor climatic conditions are unfavourable for dispersal flight activity or colony foundation (Scheffrahn et al. 2009). As such, the nuptial flights that were observed in Brussels on several occasions during two consecutive years (2020–2021) occurred exclusively indoors. So far, *R. banyulensis* has only been reported from small populations in France and Spain (Clément et al. 2001) and it is not reported as an invasive or pest species. At present, climate conditions in Belgium are unsuitable for colonies of *C. brevis* or *R. banyulensis* to establish outside. Both infestations were discovered in residential complexes in Brussels (Brussels Capital Region), since then (2020–2021) one *C. brevis* infestation has been reported in Arlon in local media (personal communication Philippe Wegnez), suggesting that the presence of termites in Belgium might have been overlooked in the past.

The infestation by *R. flavipes* at the premises of the zoo in Brugelette is much more severe. This species is often imported to new sites with infested wood, plants or plant material (Gay 1967; Ghesini et al. 2010), and has traits



Figure 2. NJ-tree of COI sequences of the subfamily Heterotermitinae (family Rhinotermitidae), using *Globitermes sulphureus* and *Pericapritermes nitobei* (family Termitidae) as outgroup (Tamura-Nei distance model, 1,000 bootstrap replicates, 70% cut off threshold). Bootstrap values are indicated at the branch nodes. Sequences were collapsed in species-clusters for readability. New sequences are indicated in red. *Reticulitermes santonensis* (= *R. flavipes*) is indicated in orange.

that are advantageous to rapid spread and establishment (Dronnet et al. 2005; Perdereau et al. 2010, 2011). It is capable of long range dispersal, which may be facilitated by human transportation (Gay 1967; Perdereau et al. 2019; Eyer et al. 2021). Recently, a connection between the spread of *R. flavipes* in

Europe and the French railways has been suggested (Andrieu et al. 2017; Baudouin et al. 2018; Suppo et al. 2018). *Reticulitermes flavipes* can persist in underground colonies and occurs in pine forests in France (Dronnet et al. 2005). The species was recently also found in the Netherlands (de Visser et al. 2023), indicating its ability to survive in similar climate conditions as Belgium. The infestation at Brugelette therefore needs to be exterminated as soon as possible and the area monitored closely to avoid any spread of this highly invasive species to other locations.

Authors' contribution

Ann Vanderheyden: writing original draft, data analysis and interpretation. Wouter Dekoninck: investigation and data collection, writing review and editing. Nathalie Smits: writing review and editing. Anicée Lombal: writing review and editing. Marc De Meyer: writing review and editing. Thierry Backeljau: writing review and editing.

Acknowledgements

We are indebted to Georges Roobaert, the family Gohin and Bram D'hondt (INBO) for providing us details on the infestations. We want to thank Catherine Vancsok, scientific Advisor of the Pairi Daiza Foundation for the authorisation to sample in the greenhouses in Pairi Daiza, Brugelette and Charlotte Taelman for her assistance during this sampling. We also thank Prof. Dr. Yves Roisin for his help with the morphological identification. Finally, the authors are thankful to all the reviewers of this manuscript.

Funding

The Barcoding Facility for Organisms and Tissues of Policy Concern (BopCo – <http://bopco.myspecies.info/>) is financed by the Belgian Science Policy Office (Belspo) under contract no. RT/23/BopCo-CE “Towards a Belgian Expert Centre for the Identification of Biological Specimens and Products of Policy Concern”.

References

- Austin JW, Szalanski AL, Scheffrahn RH, Messenger MT, Dronnet S, Bagnères AG (2005) Genetic evidence for the synonymy of two *Reticulitermes* species: *Reticulitermes flavipes* and *Reticulitermes santonensis*. *Annals of the Entomological Society of America* 98: 395–401, [https://doi.org/10.1603/0013-8746\(2005\)098\[0395:GEFTSO\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2005)098[0395:GEFTSO]2.0.CO;2)
- Austin JW, Szalanski AL, Myles TG, Borges PAV, Nunes L, Scheffrahn RH (2012) First record of *Reticulitermes flavipes* (Isoptera: Rhinotermitidae) from Terceira Island (Azores, Portugal). *Florida Entomologist* 95: 196–198, <https://doi.org/10.1653/024.095.0131>
- Baudouin G, Bech N, Bagnères AG, Dedeine F (2018) Spatial and genetic distribution of a north American termite, *Reticulitermes flavipes*, across the landscape of Paris. *Urban Ecosystems* 21: 751–764, <https://doi.org/10.1007/s11252-018-0747-9>
- Becker VG, Kny U (1977) Überleben und Entwicklung der Trockenholz-Termite *Cryptotermes brevis* (Walker) in Berlin. *Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz* 50: 177–179, <https://doi.org/10.1007/BF02156725>
- Bertelsmeier C (2021) Globalization and the anthropogenic spread of invasive social insects. *Current Opinion in Insect Science* 46: 16–23, <https://doi.org/10.1016/j.cois.2021.01.006>
- Borges PAV, Guerreiro O, Ferreira MT, Borges A, Ferreira F, Bicudo N, Nunes L, Marcos RS, Arroz AM, Scheffrahn RH, Myles TG (2014) *Cryptotermes brevis* (Isoptera: Kalotermitidae) in the Azores: Lessons after 2 yr of monitoring in the archipelago. *Journal of Insect Science* 14: 1–7, <https://doi.org/10.1093/jisesa/ieu034>
- Cao R, Su NY (2016) Temperature Preferences of Four Subterranean Termite Species (Isoptera: Rhinotermitidae) and Temperature-Dependent Survivorship and Wood-Consumption Rate. *Annals of the Entomological Society of America* 109: 64–71, <https://doi.org/10.1093/aesa/sav095>
- Clément JL, Bagnères AG, Uva P, Wilfert L, Quintana A, Reinhard J, Dronnet S (2001) Biosystematics of *Reticulitermes* termites in Europe: Morphological, chemical and molecular data. *Insectes Sociaux* 48: 202–215, <https://doi.org/10.1007/PL00001768>
- de Visser V, Noordijk J, Brooks M, Kuiper A (2023) Vestiging en overlast van de grondgebonden termiet *Reticulitermes flavipes* in Nederland. *Entomologische Berichten* 84(4): 86–91

- Dronnet S, Chapuisat M, Vargo EL, Lohou C, Bagnères A-G (2005) Genetic analysis of the breeding system of an invasive subterranean termite, *Reticulitermes santonensis*, in urban and natural habitats. *Molecular Ecology* 14: 1311–1320, <https://doi.org/10.1111/j.1365-294X.2005.02508.x>
- Emerson AE (1936) Distribution of Termites. *Science* 83: 410–411, <https://doi.org/10.1126/science.83.2157.410>
- Evans TA (2021) Predicting ecological impacts of invasive termites. *Current Opinion in Insect Science* 46: 88–94, <https://doi.org/10.1016/j.cois.2021.03.003>
- Eyer PA, Blumenfeld AJ, Johnson LNL, Perdereau E, Shults P, Wang S, Dedeine F, Dupont S, Bagnères AG, Vargo EL (2021) Extensive human-mediated jump dispersal within and across the native and introduced ranges of the invasive termite *Reticulitermes flavipes*. *Molecular Ecology* 30: 3948–3964, <https://doi.org/10.1111/mec.16022>
- Feytaud MJ (1924) Le Terme de Saintonge. *Comptes Rendus des Séances de l'Académie des Sciences* 178: 241–244
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299
- Fontana P, Buzetti FM (2003) Nuova segnalazione di *Cryptotermes brevis* (Walker, 1853) in Italia settentrionale (Insecta, Isoptera, Kalotermitidae). *Bollettino del Museo Civico di Storia Naturale di Venezia* 54: 35–44
- Gay FJ (1967) Species Introduced by man. In: Krishna K, Weesner FM (eds), *Biology of Termites*, Vol. 1. Academic Press, New York and London, pp 459–491, <https://doi.org/10.2307/1932787>
- Ghesini S, Messenger MT, Pilon N, Marini M (2010) First report of *Reticulitermes flavipes* (Isoptera: Rhinotermitidae) in Italy. *Florida Entomologist* 93: 327–328, <https://doi.org/10.1653/024.093.0233>
- Ghesini S, Puglia G, Marini M (2011) First report of *Coptotermes gestroi* in Italy and Europe. *Bulletin of Insectology* 64(1): 53–54
- Ghesini S, Müller G, Marini M (2020) First record of the subterranean termite *Reticulitermes grassei* in Switzerland. *Bulletin of Insectology* 73(1): 149–151
- Hernández-Teixidor D, Suárez D, García J, Mora D (2019) First report of the invasive *Reticulitermes flavipes* (Kollar, 1837) (Blattodea, Rhinotermitidae) in the Canary Islands. *Journal of Applied Entomology* 143: 478–482, <https://doi.org/10.1111/jen.12592>
- Kollar V (1837) Naturgeschichte der schädlichen Insekten. *Verhandlungen der K. K. Landwirtschaft Gesellschaft in Wien* 5: 411–413
- Kutnik M, Uva P, Brinkworth L, Bagnères AG (2004) Phylogeography of two European *Reticulitermes* (Isoptera) species: The Iberian refugium. *Molecular Ecology* 13: 3099–3113, <https://doi.org/10.1111/j.1365-294X.2004.02294.x>
- Liotta G (2005) Le termiti agenti di degrado delle strutture lignee dei beni culturali. In: Tampone G (ed), *Proceedings of the International Conference "Conservation of Historic Wooden structures"*, Florence, 22–27 February 2005, Vol. 1, Alter Ego Ing Arch S.r.L., a subsidiary Company of the Tuscan College of Engineers, pp 3–10
- Lo N, Kitade O, Miura T, Constantino R, Matsumoto T (2004) Molecular phylogeny of the Rhinotermitidae. *Insectes Sociaux* 51: 365–371, <https://doi.org/10.1007/s00040-004-0759-8>
- Nunes L, Cruz H, Fragoso M, Nobre T, Machado JS, Soares A (2005) Impact of drywood termites in the Islands of Azores. In: IABSE Symposium: Structures and Extreme Events, Lisbon, Portugal, 14–17, September 2005. International Association for Bridge and Structural Engineering (IABSE), pp 114–120, <https://doi.org/10.2749/222137805796271422>
- Nunes L, Gaju M, Kreckek J, Molero R, Teresa Ferreira M, de Roca CB (2010) First records of urban invasive *Cryptotermes brevis* (Isoptera: Kalotermitidae) in continental Spain and Portugal. *Journal of Applied Entomology* 134: 637–640, <https://doi.org/10.1111/j.1439-0418.2009.01490.x>
- Perdereau E, Bagnères AG, Dupont S, Dedeine F (2010) High occurrence of colony fusion in a European population of the American termite *Reticulitermes flavipes*. *Insectes Sociaux* 57: 393–402, <https://doi.org/10.1007/s00040-010-0096-z>
- Perdereau E, Dedeine F, Christidès JP, Dupont S, Bagnères AG (2011) Competition between invasive and indigenous species: An insular case study of subterranean termites. *Biological Invasions* 13: 1457–1470, <https://doi.org/10.1007/s10530-010-9906-5>
- Perdereau E, Bagnères AG, Bankhead-Dronnet S, Dupont S, Zimmermann M, Vargo EL, Dedeine F (2013) Global genetic analysis reveals the putative native source of the invasive termite, *Reticulitermes flavipes*, in France. *Molecular Ecology* 22: 1105–1119, <https://doi.org/10.1111/mec.12140>
- Perdereau E, Baudouin G, Bankhead-Dronnet S, Chevalier Z, Zimmermann M, Dupont S, Dedeine F, Bagnères AG (2019) Invasion dynamics of a termite, *Reticulitermes flavipes*, at different spatial scales in France. *Insects* 10: 1–16, <https://doi.org/10.3390/insects10010030>
- Raineri V, Rey A, Marini M, Zaffagnini V (2001) Un nuovo rinvenimento di *Cryptotermes brevis* in Italia (Isoptera). *Bollettino della Società Entomologica Italiana* 133(2): 99–102

- Roisin Y (2020) Ordre des Dictyoptera (Dictyoptères), Clade des Isoptera (Termites). In: Aberlenc HP (eds), *Les Insectes du Monde* (tome 1). Biodiversité, Classification, Clés de détermination des familles. Quae, pp 461–470
- Rust MK, Cabrera BJ (1994) The effects of temperature and humidity on the movement of the Western Drywood Termite. California Department of Consumer Affairs, 24 pp
- Scheffrahn RH, Su N-Y (1994) Keys to Soldier and Winged Adult Termites (Isoptera) of Florida. *The Florida Entomologist* 77: 460–474, <https://doi.org/10.2307/3495700>
- Scheffrahn RH, Su N-Y (2014) West Indian Drywood Termite *Cryptotermes brevis* (Walker) (Insecta: Isoptera: Kalotermitidae). *Edis* 2: 7, <https://doi.org/10.32473/edis-in236-2020>
- Scheffrahn RH, Křeček J, Ripa R, Luppichini P (2009) Endemic origin and vast anthropogenic dispersal of the West Indian drywood termite. *Biological Invasions* 11: 787–799, <https://doi.org/10.1007/s10530-008-9293-3>
- Su N-Y, Scheffrahn RH (2000) Termites as Pests of Buildings. In: Abe T, Bignell DE, Higashi M (eds), *Termites: Evolution, Sociality, Symbioses, Ecology*. Springer Science & Business Media, pp 437–453, https://doi.org/10.1007/978-94-017-3223-9_20
- Vargo EL, Husseneder C (2009) Biology of subterranean termites: Insights from molecular studies of *Reticulitermes* and *Coptotermes*. *Annual Review of Entomology* 54: 379–403, <https://doi.org/10.1146/annurev.ento.54.110807.090443>
- Weidner H (1937) Termiten in Hamburg. *Zeitschrift für Pflanzenkrankheiten (Pflanzenpathologie) und Pflanzenschutz* 47: 593–596, <https://www.jstor.org/stable/43526759>