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Perspective

Fifty years of attempted biological control of termites – Analysis of a failure

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ABSTRACT

The use of pathogens as biological control agents has long been considered a promising technology for termite control. Over the past five decades, there has been a large accumulation of scientific literature on the development of control methods using various pathogens. However, despite the evidence that biological control has essentially failed, or failed to be developed, as a method for commercial termite control, this field of research remains very active. In this study, we examined 50 years of research on the microbial control of termites in order to understand why commercial products have failed to be developed and why this field of research remains so active. All (to the extent of our knowledge) of the literature published between 1960 and 2011 was evaluated to investigate any publication bias and to detect false positives in the form of overly optimistic conclusions. This re-interpretation supports the idea that the conclusions frequently expressed have been misleading to some extent, or at least overly optimistic, about the potential for application of biological control to termites. Many results obtained from bioassays with poor biological relevancy have been interpreted as promising, while few results actually support practical application. We also suggest that the failure of termite biological control and the continued research emphasis in this area resulted in part from unrealistic optimism about the potential for development of environmentally friendly methods to control termites, publication bias, and poor understanding of termite biology.

1. Introduction

Termites (Isoptera) include more than 2600 species around the world (Abe et al., 2000), but only a few of them (70–80 species) are considered of economic importance due to their damage to manmade structures and to forestry or agricultural products (Edwards and Mill, 1986; Logan et al., 1990). In recent years, there has been a large increase in the scientific literature concerning termites (Vargo and Husseneder, 2009) which reflects their economic importance and the availability of funding to support termite research. Various preventative and remedial strategies are currently used against pest species in the termite control industry (Su and Scheffrahn, 1998, 2000). Concerning subterranean termites in particular, it has been estimated that 77% of the pest control market share is represented by soil termiticide applications in the United States (Anonymous, 2002). Despite this heavy reliance upon the application of soil insecticides, future termite control technologies may need to conform to higher environmental standards (Su, 2002).

As an alternative to liquid pesticide applications, monitoring-baiting procedures with the use of chitin synthesis inhibitors have been developed (Su, 1994; Grace and Su, 2001), and are commercially available. Botanical insecticides have also been considered (Verma et al., 2009) although their use remains anecdotal. The use of predators as biological control agents has been investigated, but did not reveal any potential for commercial application (Culliney and Grace, 2000).

In developed countries, the market for microbial insecticides for various agricultural pests represents only 1% of the total crop protection market, and mostly represents the sale of *Bacillus thuringiensis* (Berliner) products (Lisansky, 1997; Lacey et al., 2001). Biological control using pathogens has long been considered a promising technology for future termite control options (Grace, 1997) because termites were assumed to live in an environment conducive to entomopathogens (Kramm et al., 1982; Rath, 2000). However, to date, no successful implementation of biological control in the termite control industry has occurred, despite the large body of scientific literature in this particular field (Logan et al., 1990; Culliney and Grace, 2000), suggesting that the effort spent to develop such products has yet to yield concrete results (Grace, 2003).

In the current study, we examined research reports on microbial control of termites for the past 50 years in a narrative review in order to summarize evidence from multiple studies. However, there is an inherent bias in science toward publication of positive

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results (Begg and Berlin, 1988; Hasenboelher et al., 2007), as such results have a much greater chance of reaching publication in peer-reviewed journals than negative results, and as researchers tend to "fish for significance" (Boulesteix, 2010). Thus, an uncritical review of the published studies may lead to an incorrect and usually overly optimistic conclusion (Sutton et al., 2000). In addition, the overall scientific literature suffers from a large accumulation of false (or overly optimistic) positive findings and a dearth of published negative findings (Ioannidis, 2005). Recent advances in the understanding of termite disease resistance mechanisms presented in a companion paper (Chouvenc and Su, 2010) raise questions about the validity and applicability of some of the positive results published within the past 50 years in the field of termite biological control. Some studies may have used protocols with poor biological relevancy and may also have improperly and optimistically interpreted the data provided.

The purpose of our review is to understand why biological control of termites using pathogens has not succeeded despite extensive research efforts and, conversely, why this field of research remains active. We discuss the different protocols used for introduction of pathogens in a termite colony, cover the history of termite biological control, re-interpret all data published since 1960, and discuss some of the biases scientists may have confronted which could contribute to the apparent failure of termite biological control.

1.1. Protocols for introduction of pathogens

Most of the research on termite biological control has followed the concepts of classical biological control of other insect pests using pathogens (Ferron, 1978; Lacey et al., 2001). Due to the cryptic habitat and social organization of termites, however, biological control in termites has had to be modified from strategies used in agricultural crops. An inundative method was used for termite species with a central nest structure, one-piece nesting type, or intermediate nesting type (Abe, 1987). For example, drywood termites, and some dampwood and mound-building termites often, but not always, have a localized central nest where most of the individuals of a colony can be treated (Grace et al., 2009). This method has been used to demonstrate that when most of the termites are accessible for inundative treatment, it is possible to eradicate the colony (Hänel and Watson, 1983; Danthanarayana and Vitharana, 1987; Lenz and Runko, 1992, 1995; Jackson et al., 2010), although some technical limitations can be encountered and colony control can be inconsistent. A colony is defined here as a group of individuals of the same species sharing an interconnected gallery system. Such methods employ pathogens as a bioinsecticide, and transmission among individuals is not necessary.

Unfortunately, the inundative method is not realistic for termite species with a diffuse nest structure (extended nesting type), such as subterranean termites, because only a small fraction of the colony is accessible. Occurrence of an epizootic in subterranean termite species relies upon transmission of the pathogenic agent among all individuals in the colony, which is difficult due to avoidance of the treated areas by healthy individuals (Rath, 2000). Such treatments could use pathogens as a repellent for temporary protection of the treated area, but are not likely to achieve colony-level control. Therefore, alternative protocols have been deemed necessary to introduce pathogens into a subterranean termite colony. A "trap and treat" protocol was mentioned by Milner et al. (1996). This method consists of collecting individuals from a colony, treating them with a virulent entomopathogen, and releasing them back into their original nest in hopes that they will contaminate the rest of the colony. However, it is difficult to inoculate enough individuals simultaneously to trigger an epizootic within the colony (Chouvenc et al., 2008b). A baiting approach has also been considered (Delate et al., 1995; Milner, 2003; Wang and Powell, 2004), but the development of a stable and non-repellent formulation remains problematic. Despite efforts to screen for virulent strains of pathogenic agents, the delivery of sufficient inoculums to a subterranean termite colony remains an unsolved problem (Grace, 2003).

1.2. Brief history of termite biological control

Before 1960, few reports noted the pathogenic effect of microorganisms on termites. Merrill and Ford (1916) and Pemberton (1928) first reported the presence of parasitic "head inhabiting" nematodes in *Reticulitermes lucifugus* (Rossi) and *Coptotermes formosanus* Shiraki respectively, but concluded that such nematodes could not kill termites in soil conditions. De Bach and McOmie (1939) later reported the existence of two bacterial species killing laboratory colonies of *Zootermopsis angusticollis* Hagen and identified them as *Bacterium* sp. and *Serratia marcescens* Bizio. However, these authors did not discuss any potential for using such microorganisms as termite control agents. Both Kevorkian (1937) and Altson (1947) mentioned the presence of the fungus *Conidiobolus* sp. on *Nasutitermes* sp. and *Coptotermes* sp. respectively, also without mentioning any potential as a biological control agent.

In 1958, facing the emergence of *Reticulitermes flavipes* (Kollar) (Syn. *R. santonensis* Feytaud) as a structural pest in the south of France, the *Service de Pathologie des Insectes* from the *Institut Pasteur* in Paris requested a survey of potential disease agents that could be used as biological termiticides. Toumanoff and Toumanoff (1959) conducted the survey and reported that *S. marcescens* could kill termites, but discussed the problem of testing pathogens against laboratory groups of termites with "low vigor". This short report marked the debut of termite biological control research and triggered a series of studies supporting the use of pathogens to kill termites, mainly in the United States. Beal and Kais (1962) identified *Aspergillus flavus* Link as a fungal pathogen of *Reticulitermes* sp. and Lund (1962, 1965b, 1969) suggested that *Serratia* sp. and *Aspergillus* sp. could be used for termite control. Lund (1965a) reported the first field study using *S. marcescens* against *R. flavipes* and stated that termite activity ceased in the treated areas. Smythe and Coppel (1965) showed that *R. flavipes* could be susceptible to a formulation of *B. thuringiensis* and also showed that *Isaria* sp. (syn. *Paecilomyces* sp.) could be pathogenic to *R. flavipes* (Smythe and Coppel, 1966). Page (1966) suggested that *Entomophthora virulenta* Hall and Dunn, in association with *B. thuringiensis*, could be used to control *C. formosanus* in Hawaii. Meanwhile, Toumanoff (1965, 1966) screened several species of entomopathogenic fungi and bacteria, and Toumanoff and Rombaut (1965) concluded that *Metarhizium anisopliae* (Metsch.) Sorokin and *Beauveria bassiana* (Balsamo) Vuill. were the two most virulent entomopathogenic microorganisms against *R. flavipes*. At this time, the potential economic value of termite biological control appeared obvious. Lund (1966) patented formulations of *A. flavus* and *S. marcescens*, and Page (1967) patented the combination of *E. virulenta* and *B. thuringiensis* as biological control agents against termites. However, Lund (1971) concluded in a short report that none of his field studies with various pathogens demonstrated sufficient pathogenicity to termites.

In the late 1960s through early 1970s, interest in the use of pathogens against termites continued to increase (Yendol and Rosario, 1972), as indicated by the growing number of publications in this field (Fig. 1). In Hawaii, Tamashiro (1968) proposed to the US Navy to investigate the effect of various pathogens against *C. formosanus*, including nematodes (*Steinernema* spp.) and fungi (*M. anisopliae* and *B. bassiana*). This project was the beginning of an active program in termite research at the University of Hawaii, and several graduate students focused their studies on

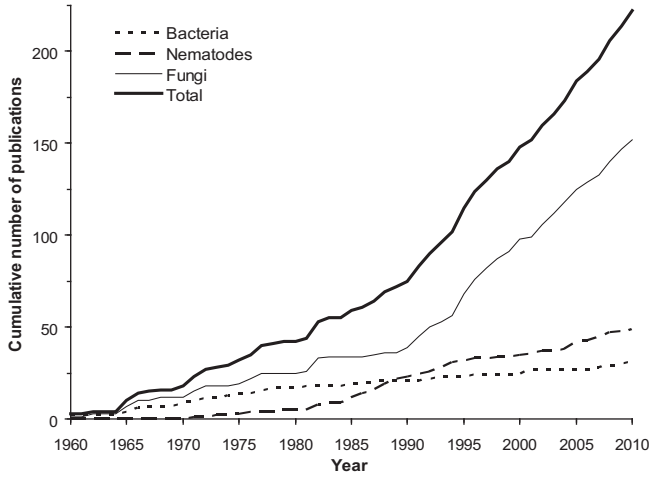

Fig. 1. Cumulative number of reports on biological control of termites (Isoptera) between 1960 and 2010.

termite-pathogen relationships (Leong, 1966; Fujii, 1975; Lai, 1977) and other aspects of *C. formosanus* biology (Su, 1982). However, Reese (1971) reported some of their preliminary data and mentioned the lack of positive results with field trials despite promising laboratory bioassays, which was later confirmed by Tamashiro (1976). In the USSR, Stadykov (1970) initiated the development of biopesticides to control *Anacanthotermes ahngerianus* Jacobs, which led to a series of publications on *Bacillus cereus* Frankland and Frankland and *B. bassiana* formulations. Field trials with these pathogens, however, showed low mortality in the treated termite colonies (Kakaliyev and Saparliyev, 1975). In Czechoslovakia, Krejzová (1971, 1972, 1975, 1976, 1977) published a series of articles testing various species of fungi against *R. lucifugus* under laboratory conditions. In Pakistan, Khan et al. (1977a,b, 1978) focused on the use of bacteria, especially *B. thuringiensis,* in an effort to develop a biopesticide against two termitid species, but no field implementation was reported.

By the early 1980s, despite the accumulation of 50 reports showing the virulence of pathogens against termites in the laboratory, no field bioassay had provided positive data supporting biological control. Kramm et al. (1982) suggested that termites exhibited behavioral mechanisms that reduced the possibility of epizootics. The 1980s were also a time of transition in commercial termite control practices. The organo-chlorine pesticides chlordane, dieldrin, aldrin and heptachlor had been widely used in the United States since 1948 for termite control in urban areas, as well as in crop protection. Concerns over the impact of chlordane on human health and the environment led the US Environmental Protection Agency (EPA) in 1978 to cancel its use on food crops and to phase out other above-ground uses over the following five years. The EPA allowed continued use of chlordane as a soil insecticide against termites in structures for an additional five years. In 1988, all previously approved uses of chlordane in the United States were canceled by the EPA (http://www.epa.gov). As of 1983, the termite control industry was aware of the need for the development of alternative control methods to replace this popular insecticide (La Fage, 1986). The development of a "green" pesticide, an environmentally friendly method to kill termites, appealed to both researchers and consumers. In this context of chemophobia, some people tried to benefit from the situation. For example, the marketing of entomopathogenic nematodes in the United States, with very little data to support their efficacy as biological control agents against termites, quickly became a controversial issue in the pest control industry (Mix, 1985, 1986; Hall, 1986). However, Epsky and Capinera (1988) and Mauldin and Beal (1989) reported the lack of success using nematodes against subterranean termites in laboratory and field studies, which essentially ended the controversy.

Outside of the United States, several laboratories intensified research on termite biological control. Hänel (1981, 1982a, 1982b) tested *M. anisopliae* against Australian mound-building termites, and tested an inundative method by introducing a large amount of conidia inside the central part of a nest of *Nasutitermes exitiosus* (Hill) (Hänel and Watson, 1983). Khan et al. (1985) continued to report the potential of *B. thuringiensis* against various termite species in Pakistan, but did not provide any field assay data. Danthanarayana and Vitharana (1987) demonstrated in Sri-Lanka that live-wood termites could be killed by injecting large quantities of nematodes directly inside the branches of tea plants, but no follow up study was done and this approach was never implemented. Nematodes were also tested in China (Anonymous, 1982b).

In the 1990s, the field of termite biological control witnessed a sudden increase in activity, with about 80 reports published between 1990 and 2000 (Fig. 1). In Australia and some Pacific islands, Lenz and Runko (1992, 1995) tested fungi and nematodes against tree-infesting kalotermitids. Milner (1991) and colleagues (Milner and Staples, 1996; Milner et al., 1996, 1997a,b, 1998a,b) pursued a large-scale screening program for developing biological control for Australian termites. In Canada, Zoberi and Grace (1990) initiated a biological control project (Zoberi, 1990, 1995; Grace and Zoberi, 1992) that Grace (1994, 1995, 1997) and colleagues continued in Hawaii (Delate et al., 1995; Grace and Ewart, 1996; Jones et al., 1996). In the mid-1990s a large project for the use of biological control agents against various insect pests was initiated in Africa (Langewald and Cherry, 2000) and several studies focused on the use of fungal pathogens against African termite species (Ochiel, 1995; Gitonga, 1996; Ochiel et al., 1997; Abebe, 2002; Langewald et al., 2003). In Brazil, Fernandes and Alves (1991, 1992), Alves et al. (1995), Moino and Alves (1998), Almeida and Alves (1996, 1999), Almeida et al. (1997), Neves and Alves (1999) conducted several laboratory and field studies using *M. anisopliae* and *B. bassiana* against the mound building termite *Cornitermes cumulans* (Kollar) and *Heterotermes tenuis* (Hagen). In Japan, the use of fungi was investigated for control of *C. formosanus* (Suzuki, 1991, 1995; Yoshimura et al., 1992;Yoshimura and Takahashi, 1998), as well as in China (Chai, 1995). In the United States, Zeck (1992), Boucias et al. (1996) and Ramakrishnan et al. (1999) tested fungal pathogens against *R. flavipes* in association with the insecticide imidacloprid in order to increase termite susceptibility to infection, but no commercial application of the combined treatment was developed. A formulation of *M. anisopliae* was commercialized (Rath, 1995) under the name Bioblast™ (Ecoscience Co.) and several patents were granted (Supplemental Table 1). Several other studies, mainly using entomopathogenic fungi, were conducted in laboratories around the world (Supplemental Table 4), confirming that interest in the development of biological control for termites remained strong.

In the early 2000s, optimism about the success of the development of biological control against termites started to fade. More evidence was produced to show that termites had the ability to reduce the likelihood of epizootics (Rosengaus et al., 1998; Staples and Milner, 2000a) and Culliney and Grace (2000) concluded their review with a cautious opinion about possibilities for the future development and implementation of termite biological control. Staples and Milner (2000b) mentioned that commercial applications were technically limited and not as easy to implement as was commonly believed. Rath (2000) also discussed the use of pathogens to control termites, but reported limited efficacy in the field due to termite avoidance of treated areas, and Bioblast was removed from the market shortly thereafter. In the absence

of concrete evidence to support the effectiveness of termite biological control, Grace (2003) concluded that initiation of an epizootic in a termite nest with a biological control agent was difficult and that successful economic control of termites using entomopathogens was unlikely. Finally, despite the large amount of earlier work on biological control of termitid species in Kenya (Langewald et al., 2003), none was reported in a recent survey of the termite control practices in this part of the world (Kagezi et al., 2010) suggesting that it was never implemented.

Although Culliney and Grace (2000) and Milner (2003) indicated that termite biological control was more complicated than originally thought, new projects to test pathogens against termites continued to emerge, as the value of "green" technology regained some attention. The United States Department of Agriculture (USDA) financed a project to screen for new virulent isolates of *M. anisopliae* (http://www.ars.usda.gov/is/pr/2000/000131.htm), the United States Agency for International Development (USAID) financed similar research programs in Pakistan (Ahmed et al. 2008a, 2008b), and more than 20 laboratories around the world continued to investigate new strains of entomopathogens for control of termites (Swaran and Varma, 2003; Huang, 2004; Wang and Powell, 2004; Albuquerque et al., 2005; Gutiérrez et al., 2005; Kakde et al., 2005; Meikle et al., 2005; Santiago-Alvarez et al., 2005; Singha et al., 2006; Souza, 2006; Devi et al., 2007; Guswenrivo et al., 2007; Jayasimha and Henderson, 2007; Maketon et al., 2007; Ezz and Abd El-Latif, 2008; Rosa et al., 2008; Yu et al., 2008; Ahmed et al., 2009; Balachander et al., 2009; Dong et al., 2009; Guirado et al., 2009; Hoe et al., 2009; Liao et al., 2009; Remadevi et al., 2010; Shahina et al., 2011).

One would have thought that after the publication of the review by Culliney and Grace (2000), efforts to develop biological control of termites would have taken directions other than those involving simple screening tests. However, since Culliney and Grace (2000), more than 80 reports of laboratory studies similar to those of the 1970–1990s have been published (listed in Supplemental Tables 2–4), and represent about one third of the total number of termite biological control publications since the 1960s.

While some researchers by the early 2000s considered that biological control of termites were unlikely to succeed, some new researchers in the field of termite control did not take into account these warnings. The following re-examination of the past 50 years of scientific research was performed essentially to caution future researchers that effective classical biological control of termites is simply not realistic, as they may be on the verge of undertaking a project where many other researchers have previously failed.

2. Fifty years of termite biological control revisited

2.1. Data collection

A total of 227 publications were collected by listing and backtracking all references reporting bioassays using entomopathogens against termites between 1960 and 2011. We focused primarily on articles dealing with bacteria, nematodes, fungi and viruses. Fungal ectoparasites of termites were not included in this study as they do not have a direct pathogenic effect on their host (Gouger and Kimbrough, 1969; Blackwell and Kimbrough, 1976; Blackwell and Rossi, 1986). In addition, studies specifically focusing on the analysis of termite defense mechanisms were not included in this study, as they have been fully reviewed and discussed in a companion paper (Chouvenc and Su, 2010) and by Rosengaus et al. (2011). The collected references were categorized either as peer-reviewed publications, or as non-peer-reviewed publications (including internal reports, conference proceedings, book chapters, theses, dissertations and general press articles). The extensive data were analyzed and presented in three separate tables (Supplemental Tables 2–4). The literature reporting the use of viruses remains anecdotal, and was listed in the tables with bacteria. Some of the publications reported several bioassays using different pathogen species/strains against various termite species. We analyzed a total of 427 bioassays and each bioassay was categorized according to the pathogen species and termite species tested. The protocol used and the results obtained were established, and the conclusion stated by the authors was taken into consideration. In addition, we noticed in the literature a confusion for several articles, on who was the original author of the work and the person who actually reported the work, e.g. Tamashiro (1976) reported by Reese (1971). The tables clarified this aspect when needed.

2.2. Interpretations of bioassays

Each bioassay was categorized according to one of three possible outcomes, "positive," "negative" or "inconclusive," according to the authors' interpretation. We also specified the reasons why we shared their opinions. Cases in which we disagreed with their interpretation are discussed below (data re-interpretation).

2.2.1. Positive experiment

In this category, the authors of the experiment concluded that the results indicated that a given pathogenic agent had a high potential for development as a biological control agent for termites. When we agreed with the authors' interpretation, we also considered whether the pathogenic microorganism was virulent to termites under biologically relevant concentrations and possessed the characteristics needed to create an epizootic within a group of termites, i.e., to self-replicate, disperse and reach secondary cycling within a large group of termites. For one-piece (drywood, central nest or dampwood) termite species where the bioinsecticide approach using an inundative method was considered, high virulence with high dosage was also considered as a positive experiment.

2.2.2. Negative experiment

The authors of the experiment concluded that the results did not indicate that a given pathogenic agent had potential for development as a biological control for termites. We agreed with their statements when the pathogenic microorganism did not show significant virulence.

2.2.3. Inconclusive experiment

The authors of the experiment concluded that the results were inconclusive in supporting biological control, as they may have found significant virulence but the experimental conditions led them to interpret their results with caution. When we agreed with them, we considered that the pathogenic agent might have some potential for use in biological control, but that the protocol used had low biological relevancy or did not allow a clear positive or negative conclusion, because the agent was not shown to have the ability to create an epizootic within a group of termites. Also, for field tests, colony control could not be confirmed or was limited to partial mortality.

2.3. Data re-interpretation

This additional step was deemed necessary as it is possible that some authors may have overstated their conclusions based upon the limited data actually obtained. In many cases, we disagreed with the author's interpretation after reviewing the protocols and results obtained for each bioassay in light of current knowledge of termite biology (Chouvenc and Su, 2010). This re-interpretation led us to consider many bioassays judged to be "positive" by the

authors, as "inconclusive". Although changing the status of an experiment from "positive" to "inconclusive" may alter the conclusion originally reached by the authors, it is not necessarily a negative interpretation. In these cases, the experiment may have provided useful data in support of biological control for termites to some extent, but the results obtained with the given experimental protocol were insufficient to validate the author's claim (Supplemental Tables 2–4). In fact, most authors concluded that more work was necessary to achieve biological control, which implies that their results were incomplete in light of the complexity of termite biology, and therefore were inconclusive. We classified the reasons for our disagreement with authors' conclusions in four categories: (1) The experimental protocol was too reductive in regard to the complex biology of termites. We feel that there is a need to go beyond the Petri dish test for virulence, because killing termites in a Petri dish in a no-choice assay has little biological relevancy and remains a screening test with no direct support for field application. (2) The concentrations of the pathogen were too high. We considered that some of the concentrations used were biologically irrelevant as it is unlikely that the given microorganism has the ability to reach such a high density under natural conditions. Biologically relevant concentrations are concentrations in which the pathogenic agent may actually be applied or is able to accumulate under natural conditions if the field. Although this limit is difficult to estimate as it varies depending on the microorganism, we considered for simplification that concentrations such as 10^7 units/ml and above are not biologically relevant concentrations, due to the difficulty of exposing an entire termite colony to such high concentrations in the field. (3) No data were provided to support the claim. Some reports claimed successful termite control without providing any empirical data. (4) The variability of the results suggested a lack of consistency in the efficacy of the treatment. This lack of reliability cannot support the use of pathogens as biological control agents at the commercial level.

2.4. General observations from the re-analysis

We compiled data from 227 publications, in which a total of 427 different experiments were reported. Each publication generally focused on one type of pathogen (bacteria, fungi, nematodes, viruses) although 11 of them reported multiple experiments with more than one type of pathogen. In detail, 32 publications reported 40 experiments with bacteria, 49 publications reported 102 experiments with nematodes, 152 publications reported 280 experiments with fungi, and 5 publications reported 5 experiments with viruses. The large number (141) of first authors and hundreds of co-authors that have published at least once in the field of termite biological control shows that this field has attracted numerous researchers from different laboratories. However, 51 of these authors published only one report of a termite-pathogen experiment, and most of them were never found again in the termite literature. In addition, of the 90 remaining primary authors that published more than once in the field of termite biological control, few of them also published on any other aspects of termite biology. This suggests that, with a few exceptions, the majority of the literature on termite biological control has been contributed by researchers who did not specialize in the study of termites.

A majority of the experiments (83%) were performed under laboratory conditions (356 out of 427), and 58% of all the laboratory experiments (206 out of 356) used either *M. anisopliae* or *B. bassiana*, although at least 47 other pathogen species were tested. This shows the strong interest in these two fungal pathogen species, which continue to attract most of the attention according to recent publications. Another remarkable observation was that, while at least 57 termite species from 27 genera were tested for susceptibility to infection by pathogens, 61% of all the laboratory experiments (217 out of 356) were performed against species of *Coptotermes* or *Reticulitermes*, demonstrating a strong interest in using biological control against termites with important pest status.

Most laboratory experiments (90%) used Petri dishes or the equivalent (well plates, small jars, etc.) for virulence tests (320 out of 356) without any other type of bioassay. For most laboratory experiments using Petri dishes, the authors concluded that their results were "positive" simply based on the virulence test. When results were considered to be "inconclusive" or "negative" by the authors, the experiment was usually not published alone, but was part of a larger screening effort. These screenings tested multiple pathogen species, and the low virulence of some pathogens was included in the report to emphasize the high virulence of another pathogen. As a result, most laboratory bioassays interpreted by their authors as "negative" or "inconclusive" were actually used to support the concept of biological control, by means of comparison with more virulent agents or strains referenced in the same study. This supports the view held by Boulesteix (2010) that one of the only ways to present negative results to the scientific community is to include them in a comparative study. Therefore, the accumulation of laboratory results leading to negative (57) and inconclusive (105) interpretations remained unnoticed due to the authors' strong emphasis on other positive interpretations (194) in these publications.

After our re-interpretation of the biological relevancy of the laboratory assays, we observed that very few studies demonstrated effective biological control of termites (Supplemental Tables 2–4). Of the 194 laboratory experiments judged as positive by the authors, we re-interpreted 166 experiments (86%) as inconclusive and only 28 remained positive according to our definitions. Most of these experiments (27 out of 28) were performed on termite species with mounds or a central nest structure. This may support the hypothesis that biological control for termites only works with inundative methods for termite species where most of the nest is accessible for treatments. Only one study on subterranean termites (Delate et al., 1995) showed promising results as the authors used a choice test protocol, although the formulation showed limited stability.

We observed a trend with respect to publication outlets; 75% of the laboratory experiments were published in peer-reviewed journals (268 out of 356) while only 38% of the field experiments were published in peer-reviewed journals (27 out of 71). This may suggest that it is difficult to publish field experiments through the peer-review system, in comparison to laboratory virulence tests, or may indicate that the authors felt that their field results were preliminary in nature and far from conclusive. In addition, of the field experiments that were interpreted as "positive" by the authors, only those against species with a one-piece nest type could be considered "positive" after our re-interpretation, while we considered all other field trials to be inconclusive. It appears that, because most of the field studies investigating biological control could not clearly support a positive outcome, and results were therefore considered by the authors to be somewhat negative despite optimistic conclusions, they were reported in non-peer reviewed outlets.

2.4.1. Bacteria

Bacteria were the first candidates evaluated for use in termite biological control (Toumanoff and Toumanoff, 1959; Lund, 1962; Smythe and Coppel,1965) but never received serious consideration for field application. Lund (1971) simply mentioned the absence of positive field results with all the different pathogens he previously screened (Lund, 1965a), including *S. marcescens*. *B. cereus* was tested in the USSR (Kakaliyev and Saparliyev, 1975), with limited documentation to support field efficacy. All 34 laboratory experiments with bacteria were conducted in Petri dishes and the concentrations of the innoculum were usually too high to be biologically relevant (Supplemental Table 2).

Very few studies were performed with bacteria after the 1980s (Osbrink et al., 2001). Among them, Connick et al. (2001) combined the use of *S. marcescens* with an immune inhibitor in order to render termites more susceptible to the bacteria, but the results were inconclusive. Recently, Devi et al. (2007) screened new bacterial species that have the potential to produce hydrogen cyanide, but again, their transfer among termites under field conditions was not discussed nor was their potential repellency (Devi and Kothamasi, 2009). Finally, Grace (2003), Husseneder and Grace (2005) and Husseneder and Collier (2009) proposed genetic modification of nonpathogenic symbiotic bacteria to create novel biological control agents (carriers of lethal genes or toxins), but these ideas have yet to extend beyond laboratory tests. The use of a genetically modified *Enterobacter cloacae* (Jordan) Hormaeche and Edwards was tested in the laboratory (Zhao et al., 2008) and showed promise, but the protocol used for the field test (Zhang et al., 2010) did not allow confirmation of colony-level control.

After re-interpreting the data concerning the use of bacteria against termites, only two experiments could be considered "positive", and these two trials were performed on a drywood (one piece) termite species (Khan et al., 1977b, 1981) where injections of large quantities of bacteria inside termite-infested wood could potentially provide control, although no field assays were reported.

2.4.2. Viruses

The use of viruses remains limited in the termite biological control literature. The presence of viruses has been reported in termites with basic virulence tests, but none of the five publications reported sufficient information to support the feasibility of biological control with viruses (Supplemental Table 2). Chouvenc and Su (2010) suggested that a good candidate for biological control of termites should have particular characteristics, among these, the capability to complete its life cycle and spread before the death of the host. Viruses would appear to fit this requirement better than any other type of pathogen and should theoretically have received more attention. The limited documentation on viruses may reflect the fact that termitologists are not typically skilled in virology, and vice versa, as virologists generally focus their work on different biological models (human health, plant disease). The lack of documentation does not necessarily reflect the absence of viruses with biological control potential, but may simply be due to lack of interdisciplinary skills and collaboration. However, one of us (J.K. Grace, unpublished) and collaborators screened numerous colonies of *R. flavipes* for viruses in the late 1980s, without success, suggesting that the limited literature may largely reflect scientific bias against the publication of negative results.

2.4.3. Nematodes

Tamashiro (1968) first proposed the use of nematodes against termites and many other researchers pursued this approach (Supplemental Table 3). Despite promising preliminary laboratory trials (Fujii, 1975), field tests using *Steinernema* sp. did not show success in killing *C. formosanus* colonies (Tamashiro, 1976). Entomopathogenic nematodes later gained popularity for biological control of various insects (Poinar, 1979), and two products containing *Steinernema* sp. were marketed as "biological termiticides" during the era immediately preceding the ban of chlordane in the United States. Press reports on novel and more environmentally benign technology in pest control promoted these products, somewhat recklessly, with an absence of supporting data (Anonymous, 1982a,b, 1983, 1985a,b). The use of entomopathogenic nematodes against subterranean termites quickly became controversial as testimonial accounts claimed success (Anonymous, 1985b; Hall, 1986), while field tests performed by USDA Forest Service researchers demonstrated negative results (Mix, 1985, 1986; Mauldin and Beal, 1989). After 1989, no further reports on the use of nematodes against subterranean termites appeared in the pest control industry press. This lack of reportage indirectly shows that nematodes ceased to be used by the pest control industry, although a chapter in "*Common-sense pest control – Least toxic solutions for your home, garden, pets and community*" edited by Olkowski et al. (1991), still advised their use to control subterranean termites. Remarkably, the use of nematodes against subterranean termites recently regained some interest (Yu et al. 2006, 2008; Ibrahim and Abd El-Latif, 2008; Shahina et al., 2011).

While nematodes appear to have a limited impact on subterranean and dampwood termites due to termite behavioral defense mechanisms (Wang et al., 2002b; Mankowski et al., 2005; Wilson-Rich et al., 2007), they have been successfully applied to control drywood termites (Kalotermitidae) where colonies are contained within a single piece of wood or a single tree. Danthanarayana and Vitharana (1987) successfully killed *Glyptotermes dilatatus* Bugnion and Popoff colonies infesting tea stems; and Lenz and Runko (1992, 1995) eliminated *Neotermes* sp. colonies from coconut palms, citrus and mahogany trees. However, these researchers found it difficult to reach entire colonies with inundative doses. Trials in the coconut palms had better results because the nest was relatively easy to locate due to the plant structure; in the tests with citrus, mahogany and other branched trees, it was difficult to apply the pathogen to the entire colony, because termites could find refuge in untreated branches (Lenz and Runko, 1992, 1995). Locating and treating all portions of the gallery system are common problems with all localized techniques for drywood termite control (Woodrow et al., 2006; Grace et al., 2009). Similarly, Amarasinghe and Hominick (1993a) showed in laboratory experiments the pathogenicity of nematodes to the drywood termite *Postelectrotermes militaris* (Desneux), but application in the field appeared inconclusive (Amarasinghe and Hominick, 1993b), confirming the difficulty of the inundative bioinsecticide approach, even for drywood termites. Finally, Rouland et al. (1996) and Benmoussa-Haichour et al. (1998) stated that nematodes were incapable of completing their life cycle in workers and soldiers of *Pseudacanthotermes spiniger* (Sjöstedt), but could complete their life cycle when infecting the alates, probably due to nutrition limitations. Therefore, it appears unlikely that nematodes could produce an epizootic in large colonies where nematodes have to be spread to all nestmates.

2.4.4. Fungi

Entomopathogenic fungi received the most attention in developing biological control for termites as 65% of all experiments reported (279 out of 427) tested a fungal species (Supplemental Table 4). More than 20 fungal species were tested for pathogenicity (outside of ectoparasites), and about 15 of them showed significant virulence when tested against various termite species in Petri dishes. However, most of the bioassays focused on the use of *M. anisopliae* (52% of all fungal experiments) and *B. bassiana* (26% of all fungal experiments).

Despite the interest in developing fungi for biological control applications, most bioassays were strictly limited to screening virulent strains, as 90% of the laboratory experiments were performed using Petri dishes, and only a few laboratory studies addressed the problems inherent in such a basic protocol (Delate et al., 1995; Wang and Powell, 2004; Chouvenc et al., 2008b). Conclusions were uniformly optimistic, but most reports did not provide any experimental data to support commercial application. Field bioassays were few (51 individual trials), and a majority of them claimed positive results with very limited data to support such claims. Convincing evidence for colony control was restricted to one-piece colonies (9 trials), as previously observed with nematode field experiments (Lenz and Runko, 1992, 1995). In field trials performed on subterranean termites, many studies appeared to

overstate their results, as the data provided were not sufficient to support successful control. No clearly negative field results using entomopathogenic fungi were reported in the peer-reviewed literature, while all reports in the non-peer-reviewed literature were interpreted as inconclusive.

The application of fungal pathogens within the diffuse nest of a subterranean colony remains problematic because termites can avoid areas treated with mycopesticides (Rath, 1995; Milner et al., 1998a; Mburu et al., 2009). This was described as a "learned avoidance" by Rath (2000). The "trap-and-treat" approach and the use of baits have been considered, and several authors have tried to overcome the repellency issue to increase the transmission potential of the pathogen (Delate et al., 1995; Rath and Tidbury, 1996; Staples and Milner, 2000a; Milner, 2003; Wang and Powell, 2004; Chouvenc et al., 2008b), but no applicable formulation has been successfully developed. The absence of transmission of the fungal pathogen among termites remains the major factor preventing epizootics in extended colonies. Grace and Zoberi (1992) suggested that living termites could be effective vectors of fungal conidia but fungus-killed termites were inefficient in generating transfer of conidia. Rath and Tidbury (1996) showed that dead termites sporulating fungal conidia would induce repellency, thus preventing transmission. However, it is unlikely that a cadaver would reach sporulation, because termites infected by *M. anisopliae* are quickly cannibalized or buried by nestmates (Kramm and West, 1982; Kramm et al., 1982; Strack, 2000; Rath, 2000; Chouvenc et al., 2008b). We can conclude that different social behaviors would decrease the opportunities for the fungal pathogen to be transmitted among the individuals of a colony, and interaction with termite physiological defenses would likely prevent completion of the fungal life cycle within the colony, reducing the possibility of an epizootic (Chouvenc and Su, 2010).

Milner (2003) suggested that future advances in termite biological control using fungal pathogens will come mainly from developing better formulations and strategies for use rather than from a continued search for more virulent isolates. Unfortunately, most recent studies have continued to focus on the search for virulent strains rather than developing technology to bypass termite defense mechanisms. For example, one could speculate that it would be valuable to isolate a native strain of *M. anisopliae* from China in order to develop a biological control protocol against *C. formosanus* in the United States using the enemy-release hypothesis (Torchin et al., 2003). However, *C. formosanus* is also a severe pest in its native area in southern China (Wang et al., 2002a), demonstrating that soil microorganisms naturally occurring in this region are not effective in regulating the termite population densities below an economic threshold. Therefore continued screening of microbial agents in this area would appear futile (Grace, 2003), a conclusion supported by the recent work of Husseneder et al. (2010a).

While fungal entomopathogens were long considered as the most promising candidates for biological control of termites, both Rath (2000) and Culliney and Grace (2000) pointed out the lack of good field evaluations of their efficacy, which inhibits the ability to prove or disprove their potential for biological control applications. In light of our review, we suggest that the absence of publications of such field assays suggests that no fungal pathogen has ever been a serious candidate for successful application.

3. Discussion

3.1. Laboratory results can be deceptive

Laboratory studies using a basic protocol, such as Petri-dish-style experiments, are necessary to perform original screening when looking for virulent microbial strains. Such experiments are valuable, but remain the first step of a long process in the development of a control method. Lenz (1986) stated that laboratory assessments of materials against termites provide an indication of the likely performance of these materials in the field. However, the artificial conditions in laboratory trials can affect termite vigor and behavior, and may thus lead researchers to draw conclusions based on poorly relevant results. In addition, Lenz (2009) remarked that bioassays to assess the effectiveness of biocides on subterranean termites have often not taken into consideration the complex biology of the tested species. Such bioassays and their interpretation may thus be essentially meaningless when their application to control field colonies is considered. Termite interactions with microorganisms are complex (Chouvenc et al., 2008a, 2008b, 2011; Husseneder et al., 2010b), and many researchers appear to have ignored this complexity in favor of a reductionist approach.

Laboratory conditions are much more favorable for pathogenicity than field conditions (Chouvenc et al., 2008b). In the field, diseased termites are easily avoided by healthy termites, since there are no constricting barriers and termites can simply move away from the pathogen source (Zoberi, 1995; Rath, 2000). Toumanoff and Toumanoff (1959) first reported the presence of *S. marcescens* in *R. flavipes*, and their preliminary tests showed that it was virulent to termites. However, they mentioned that "*...the gravity of infections produced by* Serratia *largely depends on the unfavorable environment for the insects...*," which indicated their caution in extrapolating from the mortality of termites in artificial environments such as Petri dishes. Similarly, Smythe and Coppel (1965) mentioned that a high dosage of *B. thuringiensis* was necessary for high mortality of *Reticulitermes* sp., and that the experimental protocol could influence the results. Petri dishes with treated filter paper at the bottom would result in high termite mortality, while the mortality was not as high when sand was used. Krejzová (1971) also showed that termite mortality could be obtained in the laboratory with high concentrations of certain fungi, but mentioned the potential difficulty of reaching such high pathogen concentrations under field conditions. These pioneering researchers in biological control emphasized that termites were sensitive to the artificial experimental environment, and they were cautious about extrapolating to field use from their limited laboratory results. Unfortunately, many subsequent researchers in biological control have been far less cautious. The potential value (both economic and environmental) of a successful "green" method of controlling termites has probably lead many researchers to be unduly optimistic when obtaining positive results from virulence tests in Petri dishes. Overall, it appears to us that the reason for the accumulations of hundreds of scientific reports claiming great potential for termite biological control is that most researchers remain at the screening step of the process and do not investigate further with more biologically relevant protocols, or fail to report such investigations.

It is always possible to kill termites in a Petri dish with any potential microbial agent, given a sufficiently high concentration. Thus, results with microorganisms that are "pathogenic" or "highly virulent" when used at biologically irrelevant concentrations end up being published as "showing great promise" to control termites. Such publication inevitably leads to an accumulation of questionable positive results about the potential of termite biological control. In extrapolating from unrealistically high laboratory concentrations of pathogens to field potential, the most elementary concept of toxicology is unfortunately frequently ignored: "*dose makes the poison*" (Paracelsus, 1538). In addition, many publications have employed a photo of a termite, infested by a given pathogen, to support conclusions concerning the virulence of the pathogen. While the visual effect of a pathogen on termites can be impressive, it does not necessarily indicate much concerning its potential as a biological control agent, since, as in the case

Fig. 2. Growth of *Aspergillus nomius* on a dead alate of *Coptotermes gestroi*. Although visually impressive, *A. nomius* grows as a saprophyte. (*Source:* Thomas Chouvenc)

illustrated in Fig. 2, the dramatic image may be elicited by a weak pathogen or a saprophyte.

3.2. Inundative methods have limited application

Several studies have shown that it is possible to kill termite colonies using an inundative method, if most of the individuals within the colony are accessible for direct treatment (Danthanarayana and Vitharana, 1987; Lenz and Runko, 1992; Lenz, 2005). This method has mainly been applied against tree-infesting termites in agricultural or forestry situations, and against some mound-building termites. However, colony control using such a protocol may be unreliable (Hänel and Watson, 1983; Amarasinghe and Hominick, 1993b; Lenz and Runko, 1995; Singha et al., 2011) because parts of a given colony can survive the treatment. In addition, Lenz et al. (2000) mentioned that the successful application of such protocols depends upon several factors including the funding and the available manpower. Cowie et al. (1989) went further in stating that "*these techniques are labor-intensive and therefore expensive and not appropriate for large-scale use in forestry*," indicating that the effort necessary to achieve control may not be cost effective, or reliable. Finally, the inoculation of large quantities of a given pathogen using inundative methods may also negatively impact other non-target insect populations, but such considerations have rarely been taken into account, and the interactions between entomopathogenic agents and non-target insect species remain poorly documented (Roy et al., 2009; Hesketh et al., 2010).

Although some laboratory and field experiments showed promise for the biological control of Kalotermitidae and mound-building termites, the difficulty of inundative applications in the field has prevented the actual use of these methods. The case of *C. cumulans* in Brazil is an instructive example, as Fernandes and Alves (1991) showed that this mound-building termite could be controlled in the field using fungal pathogens with an inundative protocol. Additional field and laboratory trials followed this original report (Fernandes and Alves, 1992; Alves et al., 1995; Neves and Alves, 1999, 2000a, 2000b, 2004; Guirado et al., 2009; Toscano et al., 2010), and most of these supported the use of *M. anisopliae* and *B. bassiana* as biological control agents against *C. cumulans*. However, 20 years after the publication of the original field results and the repetitions of such "success," the biological control of *C. cumulans* remains at the experimental stage.

3.3. Subterranean termites can prevent epizootics

Keller and Zimmermann (1989) reviewed the theoretical and applied epizootiology of mycopathogens infecting soil insects and concluded that, despite the favorable habitat for insect-pathogenic fungi, few epizootics were noted, mainly due to the cryptic nature of soil insects. While a majority of termite biological control studies have focused on the use of pathogens against pest species of subterranean termites, their control has never been achieved through the use of pathogens. Chouvenc and Su (2010) reviewed disease resistance mechanisms found in subterranean termites and suggested that interactions among these mechanisms reduce the likelihood of pathogens completing their life cycle within the colony, which supports the hypothesis that the homeostatic colony environment of social insects tends to reduce the virulence of potential parasites (Hughes et al., 2008). The absence of replication of the pathogenic agent remains problematic as this is a strong mitigating factor against the success of the microorganism (Husseneder and Grace, 2005). Thus, in subterranean termites, initiation of an epizootic and successful control is unlikely with the use of pathogens alone (Grace, 2003; Chouvenc and Su, 2010). Finally, it has been shown that subterranean termites possess a heavy bacterial cuticular load that includes few entomopathogens (Husseneder et al., 2010b), which also supports the idea that the subterranean termite nest does not favor the presence of pathogens (Chouvenc et al., 2008b, 2011).

Because defense mechanisms prevent epizootics, it has been suggested that inhibiting these defense mechanisms could render termites more susceptible to infections (Boucias et al., 1996; Connick et al., 2001; Bulmer et al., 2009). Several studies have tried to use sub-lethal concentrations of the insecticide imidacloprid in order to reduce the grooming activity of subterranean termites and allow fungal pathogens to initiate an epizootic (Zeck, 1992; Almeida and Alves, 1996; Boucias et al., 1996; Almeida et al., 1998; Moino and Alves, 1998; Ramakrishnan et al., 1999). However, this method encountered the problem of delivery of insecticides to termite individuals at a distance from the application site (Su, 2005). In addition, as pointed out by Zeck (1992), if sublethal concentrations of imidacloprid could be applied to impact the majority of termites in the colony, it would be unnecessary to introduce a biological control agent since endemic pathogens would likely control the stressed colony. It should be noted that this approach negates an important argument for the use of biological control agents in order to reduce pesticide applications.

The combination of microbes and pesticides has been presented as an integrated pest management (IPM) solution for several agricultural pests, although many practices claimed as IPM strongly rely on pesticide application for efficacy (Debach and Rosen, 1991). The concept of IPM in termites, as described by Su and Scheffrahn (1998), is not just a mixture of synergistic tools. Rather, it needs to provide cost effective protection against termite damage. Multiple applications of insecticides and pathogens may require more effort for formulation, shipping, and application than current practices with baits and soil insecticides. Therefore, it is difficult to consider such an approach IPM, and the absence of field efficacy

data and commercial application after promising experimental work tends to support our argument that this is an unlikely route to an epizootic.

3.4. Human factors involved in the failure

In addition to the technical limitations, which suggest that termite biological control is not feasible in its current form, we also believe that human factors are at least partially responsible for the recurrent absence of success of termite biological control.

3.4.1. Motivation bias

Biological control has always been an attractive goal for pest management (Olkowski et al., 1991). Concerns over long-term damage to the environment from extensive use of insecticides have grown in public and political debates, and "green" strategies are viewed favorably by some consumers. Social pressure to reduce the use of pesticides has promoted the idea that a control solution compatible with environmental protection is generally the best option. As a result, the "green" argument has induced a bias in the acceptance of the potential of biological control, with little (Shah and Pell, 2003) or no evidence for such a claim. If one is biased toward such an approach for both rational and emotional reasons, positive preliminary results in the laboratory could easily lead one to overstate conclusions. The challenge for a researcher in this area is to transform ideas to practice while remaining strictly dispassionate when interpreting the data.

3.4.2. Publication bias

In a book chapter, Langewald et al. (2003) mentioned many bioassays performed in Africa that were never reported in any accessible literature, and a screening for viruses by one of us was never reported (J.K. Grace, unpublished). While we were gathering the literature on termite biological control, we encountered difficulties in accessing a large portion of "grey literature" mainly from China, South East Asia, and Africa; reports that are often poorly or wrongly cited, are not included in most scientific indices, or are in the form of conference abstracts that were not intended for citation. This may have contributed to the publication bias we observed in our review.

Academic research also depends heavily on the ability to obtain extramural funding. In the biomedical field, for example, there is documentation that sponsored studies tend to favor the outcome preferred by the sponsor (Yaphe et al., 2001; Lesser et al., 2007; Rowe et al., 2009), resulting in a publication bias. Similarly in our review, some researchers may have been overly positive about their results in order to maintain or obtain future funding. It is also possible that some researchers may have refrained from publishing negative results as it could hinder the chances for future funding. In addition to this, reviewers are generally not kind to negative results which may also limit the opportunity to publish such results under the peer-review system. While 356 laboratory experiments were published mostly in the peer-reviewed literature, only 71 field experiments were reported, mostly in non peer-reviewed literature, with very little concrete data to support the application of biological control against termites. Paradoxically, greater publication of negative field results in the peer-reviewed literature would be much more valuable for science than the reporting of numerous positive laboratory pathogenicity tests. Publication of well-conducted studies with negative results may be more useful than commonly assumed by journals and reviewers (Boulesteix, 2010).

3.4.3. Lack of background in termite biology

While the list of authors who published on termite biological control is long (at least 141 different first authors and several hundreds of additional co-authors), very few published on any other aspect of termite biology. Many were originally microbiologists or general entomologists, and in some case neither of these. In many cases, application of the classical concepts of biological control (Tanada and Kaya, 1993) to termites was made under the assumption that what worked for solitary insects would also work for termites, not taking into account the fact that termites are social insects with a complex biology (Chouvenc and Su, 2010). Worse, the inaccurate assumption that the conditions inside a termite nest would improve transmission of disease remains strong in the belief of many, even in the most current literature, as discussed in Chouvenc and Su (2010) and Husseneder et al. (2010b). This unfortunately has lead many authors, unfamiliar with termite biology, to take an inappropriate approach to the problem and to repeat the mistakes of previous authors. We therefore suggest that future researchers in this field carefully take into account the current knowledge of termite biology, in order to avoid simplistic assumptions and interpretations.

3.4.4. Legal limitation

In some areas of the world the use of microbes for pest control is highly restricted, making field tests difficult. Field studies with living organisms are subject to specific regulations in the USA, and testing and use of non-endemic microbes are difficult in Hawaii due to the conservation status of the islands (J.K. Grace, *pers. obs.*). Although the motivation, expertise and opportunity may be present to perform field studies of entomopathogenic agents against termites, legal restrictions could still limit researchers to laboratory trials. This would obviously further reduce the likelihood of publishing field results.

3.4.5. Patent conflicts

As is often the case with pest control issues, a considerable amount of money may be at stake if there is an improved economic solution. To assure the intellectual property rights to a control method using pathogens, many have patented such procedures (Supplemental Table 1), and the number of patent applications filed (at least in the USA) shows how strong the monetary influence can be. While the scientific process encourages spreading information as widely as possible, the patent process requires absolute discretion, at least until the patent is officially granted. In addition, a patent application does not favor inclusion of negative results. The studies described in these patents are laboratory pathogenicity tests and are subject to the same limitations as the "positive" results reported in journal articles as previously described, patent applications being essentially non-refereed publications.

3.4.6. Press releases

The "green" press has also had an impact on the positive bias toward termite biological control prospects. During the 1980s in the USA, despite little information on the efficacy of entomopathogenic nematodes against termites, several distributors marketed nematodes to pest management professionals (PMPs) for use in urban situations. This was presented as "very promising technology" that could insure "high success rates" (Anonymous, 1983, 1985b; Hall, 1986; Olkowski et al., 1991), despite negative field trials (Mix, 1985, 1986; Mauldin and Beal, 1989). The claims that nematodes "work" made by some PMPs, as reported in the trade publications *The IPM Practitioner* and *Pest Control*, fueled the debate over the efficacy of nematodes (Hall, 1986), with little scientific data made available to validate or invalidate such claims. Interest in nematodes declined in the early 1990's, suggesting greater awareness of a lack of efficacy, although both the press and the technical literature were silent on this topic.

Another case where press reports have been misleading was the commercialization of Bioblast using *M. anisopliae*. Rath (1995) supported the use of this product, and Quarles (1995) wrote an

extremely positive article about this mycoinsecticide, again with little supporting data to back the claims. Quarles (1995) included in his article about Bioblast, the success of large-scale field trials gleaned from an interview with T.G. Myles (University of Toronto). However, Myles (*pers. com.*) has subsequently indicated that he was describing work performed with the bait insecticide sulfluramid, later published in Myles (1996), rather than with *M. anisopliae*. Despite good press, Bioblast was later withdrawn from the market, but again, this commercial failure went largely unnoticed.

4. Conclusion: the future of research on biological control of termites

Our re-interpretation of research of the past 50 years on the development of biological control of termites using pathogens demonstrated that this technology is currently not successful. Many studies have been overly optimistic, if not misleading, about the real potential for such application, and all efforts to date have failed to produce effective control. The review of all the available data published on termite biological control since the 1960's, without a re-interpretation of each actual result, would have suggested that this approach has great potential for commercial use. However, our re-interpretation shows that only 28 out of 356 laboratory experiments provided sufficient data to support further research (for termites with one-piece nests only), and confirms that publication bias and the accumulation of questionable positive findings has led to overestimates of the real potential for termite biological control.

Langewald and Cherry (2000) mentioned that one of the reasons for limited implementation of microbial control is the pursuance of an inappropriate model for biopesticide development, based on small research teams lacking the multidisciplinary expertise required. The accumulation of independent studies testing pathogens against termites throughout the world in the past decades and the absence of actual product development and implementation suggest that this is also true for the field of termite biological control. In addition, in many microbial control research projects, pest problems have been approached with no clear implementation route in mind (Langewald and Cherry, 2000). It was often thought that it would be easy to replace a chemical pest control product with a microbial product, but the difficulties in proceeding from research to technology transfer and implementation have prevented such success (Langewald and Cherry, 2000), a situation that also applies to research on biological control of termites (Staples and Milner, 2000b).

Recent advances in the understanding of termite defense against infection (Chouvenc and Su, 2010) have demonstrated that microbial control of subterranean termites is currently unfeasible because of the need for infectious agents to bypass various defense mechanisms in order to allow epizootics to occur. The use of paratrangensis has been considered (Husseneder and Grace, 2005; Husseneder and Collier, 2009), but this approach remains mainly theoretical. The use of immuno-suppressors has also been considered to enable pathogens to bypass the immune defenses of termites (Bulmer et al., 2009) and may indeed open possibilities for the future of biological control, but has not been fully developed or tested in the field. With respect to inundative applications for one-piece and mound-building colonies, it is technically possible to achieve control in certain cases, but it remains unrealistic for large-scale or commercial applications (Cowie et al., 1989; Lenz and Runko, 1992,1995).

The evidence from 50 years of research indicates that biological control has failed to show real promise for termite control despite the claims resulting from laboratory bioassays testing pathogens for virulence. Certainly, these are valid studies, and are necessary to obtain a pathogenic agent suitable for biological control, but claims that the results are biologically relevant to cost-effective biological control for termites at this point are extremely premature. As Grace (2003), and Chouvenc and Su (2010) suggested, so long as researchers keep insisting upon a classical approach to termite biological control, it will remain unsuccessful. Instead, by focusing research in understanding the complex biology of termites, particularly their various defense mechanisms (Bulmer et al. 2009; Chouvenc and Su, 2010; Rosengaus et al., 2011), investigators may find a way for pathogens to bypass such mechanisms, and improve prospects for biological control.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocontrol.2011.06.015.

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Supplementary data

Biological Control

2011

Fifty years of attempted biological control of termites – Analysis of a failure

By

Thomas Chouvenc, Nan-Yao Su and J. Kenneth Grace

Table 1. List of patents referencing termite biological control

Patent No.	Authors	Year	Application Publication	Title
3,249,492	Lund, A.E.	1966	N/A	Controlling termites with a fungus
3,249,493	Lund, A.E.	1966	N/A	Repelling termites with a fungus
3,249,494	Lund, A.E.	1966	N/A	Combating termites with *Aspergillus flavus*
3,337,395	Page, R.Z.	1967	N/A	Termite control by induced epizootics of entomophagous microorganisms
5,141,744	Chang, F.N., and Gehret, M.J.	1992	N/A	Insecticide delivery system and attractants
WO/004034	Gunner, H., Kane, J., Duan, H.	1994	US1993/007143	Biological control of termites
5,512,280	Johal, S.S. and Marold, M.M.	1996	N/A	Maintenance and long term stabilization of fungal conidia using surfactants
5,595,746	Milner R.J., et al.	1997b	N/A	Insect pest control
5,728,573	Sugiura et al.	1998	N/A	Termiticide and method for termite control
6,280,723	Stimac J.L. and Alves S.B.	2001	2001/0006632	Methods and materials for control of termites
N/A	Mikami K. and Yamanaka S.	2003	2003/0157062	Method for exterminating termites
N/A	Roe, D.J.	2003	2003/0014906	Method for biological control of termites
6,660,290	Stamets P.E.	2003	2004/0161440	Mycopesticides
6,660,291	Wright M.S. et al.	2003	2004/0047841	Use of *Paecilomyces* spp. As pathogenic agents against subterranean termites
6,926,889	Husseneder C. et al	2005	2002/0119556	Recombinant bacteria for use in insect control
7,037,494	Mattingly, S.J. and Johnson D.L.	2006	2003/0068304	Formulation and methods for insect control
7,122,176	Stamets P.E.	2006	2004/0213823	Mycoattractants and mycopesticides
N/A	Cates, J.	2007	2007/0256350	Apparatus and method to intercept and interdict subterranean termites using miscible tasks
WO/064614	Raina, A., Wright, M., Lax, A.	2007	US2007/112257	A strain of the fungus *Metarhizium anisopliae* for controlling subterranean termites
EP1972196	Al-amidi, A.	2008	EP20070394004	Formulation for the biological control of insect pests
7,790,151	Raina A. et al.	2010	US2006/389609	Strain of fungus *Metarhizium anisopliae* for controlling subterranean termites
7,951,388	Stamets P. E.	2011	US2009/0047236	Mycoattractants and mycopesticides

N/A= Non applicable.

Table 2a. Number of experiments testing 1 termite *sp.* against 1 bacterial *sp.*, reported in the literature, peer reviewed and non-peer reviewed.

Bacteria (32 reports, 40 experiments)	Laboratory tests[a,b]			Field tests[c]			Total
	Positive	Inconclusive	Negative	Positive	Inconclusive	Negative	
Authors' interpretation							
Peer reviewed	18	9	1	1	0	1	30
Non-peer reviewed	5	1	2	1	0	1	10
Total	23	10	3	2	0	2	40
Our re-interpretation							
Peer reviewed	2	25	1	0	1	1	30
Non-peer reviewed	0	6	2	0	1	1	10
Total	2	31	3	0	2	2	40

[a]Laboratory test = 36 experiments
[b]Petri dish = 36 experiments
[c]Field test = 4 experiments

Table 2b. Listing of experiments testing 1 termite *sp.* against 1 bacterial or viral *sp.*, reported in the literature.

Termite species	Pathogen	References	Laboratory or field[a]	protocol	Results	Authors Interpretation	Re-interpretation	Reason[b]
Termopsidae								
Zootermopsis angusticollis	*Bacillus thuringiensis*	Smythe and Coppel (1965)	L-Petri dish	Feeding/direct contact	High mortality at high dosage	Inconclusive	Inconclusive	
Zootermopsis angusticollis	*Serratia marcescens*	De Bach and McOmie (1939)	L-Petri dish	Feeding and direct injection	High mortality with direct injection	Inconclusive	Inconclusive	
Hodotermitidae								
Anacanthoterme ahngerianus	*Bacillus brevis*	Vypiyach and Voronkina (1972)*	L-Petri dish	direct contact	Low mortality	Negative	Negative	
Anacanthotermes ahngerianus	*Bacillus cereus*	Stadykov et al. (1973)	L-Petri dish	Feeding/direct contact	High mortality	Positive	Inconclusive	P
Anacanthotermes ahngerianus	*Bacillus cereus*	Kakaliyev and Saparliyev (1975)	F	Field colonies, soil treatment	No or low mortality, repellency issue	Negative	Negative	
Kalotermitidae								
Bifiditermes beesoni	*Bacillus thuringiensis*	Khan et al. (1985), also reported in Khan et al. (1981)	L-Petri dish	Feeding/direct contact, high dosage	Small groups of termites (10) dies faster than large groups (100)	Positive	Positive	
Bifiditermes beesoni	*Serratia marcescens*	Khan et al. (1977b)	L-Petri dish	Direct contact, high dosage	100% mortality in 12d	Positive	Positive	
Rhinotermitidae								
Coptotermes formosanus	*Bacillus thuringiensis*	Grace and Ewart (1996)	L-Petri dish	Feeding/direct contact with Bt encapsulated in *Ps. fluorescens*	No/low mortality with the strains used	Negative	Negative	
Coptotermes formosanus	*Enterobacter cloacae*	Zhao et al. (2008)	L-Petri dish	Feeding/direct contact, high dosage	High mortality in 29d	Positive	Inconclusive	P, C
Coptotermes formosanus	*Enterobacter cloacae*	Zhang et al. (2010)	F-bait	Baiting of all monitoring traps	No termite activity within 5 month	Positive	Inconclusive	N
Coptotermes formosanus	*Serratia marcescens*	Connick et al. (2001)	L-Petri dish	Feeding/direct contact, used with Eicosanoid Biosynthesis Inhibitor	High mortality. Kills faster when combined with EBI, but magnitude effect insufficient	Inconclusive	Inconclusive	
Coptotermes formosanus	*Serratia marcescens*	Osbrink et al. (2001)	L-Petri dish	Isolated from dead *C. formosanus* colony, 6 strains tested	Strain T8 caused 100% mortality in 19 d, when forced exposed	Inconclusive	Inconclusive	
Coptotermes gestroi	*Bacillus thuringiensis*	Sukartana et al. (2000)*	L-Petri dish	Direct contact, unknown concentrations	No/low mortality	Negative	Negative	
Coptotermes heimi	*Pseudomonas aeruginosa*	Khan et al. (1992)	L-Petri dish	Direct contact, high dosage	89% mortality in 25d	Inconclusive	Inconclusive	
Coptotermes sp.	*Bacillus thuringiensis*	Tamashiro (1968)*	L-Petri dish	Direct contact	Some mortality	Inconclusive	Inconclusive	
Heterotermes indicola	*Bacillus thuringiensis*	Khan et al. (1977a)	L-Petri dish	Direct contact, high dosage	100% mortality in 9-10d	Positive	Inconclusive	P, C
Heterotermes indicola	*Bacillus thuringiensis*	Khan et al. (1978)	L-Petri dish	Feeding/Histopathology	Infection through the gut lumen	Positive	Inconclusive	P
Heterotermes indicola	*Pseudomonas aeruginosa*	Khan et al. (1992)	L-Petri dish	Direct contact, high dosage	84% mortality in 25d	Positive	Inconclusive	P, C
Heterotermes indicola	*Serratia marcescens*	Khan et al. (1977b)	L-Petri dish	Direct contact, high dosage	100% mortality in 13d	Positive	Inconclusive	P, C
Reticulitermes flavipes	*Bacillus cereus*	Toumanoff (1966)	L-Petri dish	Feeding/direct contact	High mortality at high dosage	Positive	Inconclusive	P, C
Reticulitermes flavipes	*Bacillus thuringiensis*	Smythe and Coppel (1965)	L-Petri dish	Feeding/direct contact	High mortality at high dosage	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Bacillus thuringiensis*	Page (1966)*	L-Petri dish	In combination with *Entomophthora virulenta*	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Bacillus sp.*	Stadykov (1970)	L-Petri dish	Direct contact	High mortality at high dosage	Positive	Inconclusive	P, C
Reticulitermes flavipes	*Serratia marcescens*	Toumanoff and Toumanoff (1959)	L-Petri dish	Feeding/direct contact	Moderate mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Serratia marcescens*	Lund (1965a)*	L-Petri dish	Unknown	High mortality within 24	Positive	Inconclusive	P, N
Reticulitermes flavipes	*Serratia marcescens*	Lund (1965a)*	F	Unknown	Reduction of termite activity	Positive	Inconclusive	P, N, V
Reticulitermes flavipes	*Serratia marcescens*	Lund (1971)*	F	Unknown	No epizootic observed in the field	Negative	Negative	

Termite species	Pathogen	References	Laboratory or field[a]	protocol	Results	Authors Interpretation	Re-interpretation	Reason[b]
Reticulitermes hesperus	*Bacillus thuringiensis*	Smythe and Coppel (1965)	L-Petri dish	Feeding/direct contact	High mortality at high dosage	Inconclusive	Inconclusive	
Reticulitermes lucifugus	*Bacillus thuringiensis*	Vypiyach (1972)*	L-Petri dish	direct contact, associated with *B. bassiana*	High mortality	Positive	Inconclusive	P
Reticulitermes virginicus	*Bacillus thuringiensis*	Smythe and Coppel (1965)	L-Petri dish	Feeding/direct contact	High mortality at medium dosage	Inconclusive	Inconclusive	
Termitidae								
Macrotermes sp.	*Photorhabdus luminescens*	Shahina et al. (2011)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Microcerotermes championi	*Bacillus thuringiensis*	Jafri et al. (1974)*	L-Petri dish	Soil environment	High mortality	Positive	Inconclusive	P
Microcerotermes championi	*Bacillus thuringiensis*	Khan et al. (1977a)	L-Petri dish	Unknown	100% mortality in 10-13d	Positive	Inconclusive	P
Microcerotermes championi	*Bacillus thuringiensis*	Khan et al. (1985)	L-Petri dish	Feeding/direct contact, high dosage	Small groups of termites (10) dies faster than large groups (100)	Positive	Inconclusive	P, C
Microcerotermes championi	*Pseudomonas aeruginosa*	Khan et al. (1992)	L-Petri dish	Direct contact, high dosage	100% mortality in 25d	Positive	Inconclusive	P, C
Microcerotermes championi	*Serratia marcescens*	Khan et al. (1977b)	L-Petri dish	Direct contact, high dosage	100% mortality in 7d	Positive	Inconclusive	P, C
Odontotermes obesus	*Aeromonsa caiviae*	Devi et al. (2007)	L-Petri dish	Direct contact	Medium mortality	Positive	Inconclusive	P
Odontotermes obesus	*Alcaligenes latus*	Devi et al. (2007)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes obesus	*Pseudomonas fluorescens*	Devi and Kothamasi (2009)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes obesus	*Rhizobium radiobacter*	Devi et al. (2007)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
VIRUS (5 reports, 5 experiments)								
Cryptotermes brevis	Iridovirus	Fowler (1987)	L-Petri dish	Feeding/direct contact	High mortality	Positive	Inconclusive	P
Porotermes adamsoni	ABPV-like	Gibbs et al. (1970)	L-Petri dish	Direct injection, 3 different strains	High mortality after 8d	Positive	Inconclusive	P
Kalotermes flavicollis	NPV-like	Al Fazairy and Hassan (1988)	L-Petri dish	Feeding/direct contact	Moderate mortality	Inconclusive	Inconclusive	
Kalotermes flavicollis	NPV-like	Al Fazairy and Hassan (1993)	L-Petri dish	Feeding/direct contact	Moderate mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	EPV-like	Levin et al. (1993)	L-Petri dish	Feeding/direct contact	Moderate mortality	Inconclusive	Inconclusive	

[a]L= Lab, F= Field.

[b]Explanation for disagreeing with the authors' interpretation. P=The experiment was performed in a Petri dish or equivalent, with poor biological relevancy to the given termite species and remains a screening test. C=Mortality was observed only with high concentrations of the pathogen which cannot be applied in the field. N=No data were provided to support the claim. V=The variability in the results shows that control was not consistent.

*Non-peer reviewed journal

Table 3a. Number of experiments testing 1 termite *sp.* against 1 nematode *sp.*, reported in the literature, peer reviewed and non-peer reviewed.

Nematodes (49 reports, 102 experiments)	Laboratory tests[a,b]			Field tests[c]			Total
	Positive	Inconclusive	Negative	Positive	Inconclusive	Negative	
Authors' interpretation							
Peer reviewed	20	20	24	1	2	3	70
Non-peer reviewed	14	2	6	5	3	2	32
Total	34	22	30	6	5	5	102
Our re-interpretation							
Peer reviewed	2	37	25	1	2	3	70
Non-peer reviewed	1	15	6	1	7	2	32
Total	3	52	31	2	9	5	102

[a]Laboratory test = 86 experiments
[b]Petri dish = 73 experiments
[c]Field test = 16 experiments

Table 3b. Listing of experiments testing 1 termite *sp.* against 1 nematode *sp.*, reported in the literature.

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Mastotermitidae								
Mastotermes darwiniensis	*Heterorhabditis sp.*	Bedding and Molyneux (1982)	L-Agar plates	Immersion	Pathogenic	Inconclusive	Inconclusive	
Mastotermes darwiniensis	*Heterorhabditis sp.*	Bedding*, reported in Watson (1990)*	L	unknown	5 nematodes to kill 1 individual	Positive	Inconclusive	N
Mastotermes darwiniensis	*Heterorhabditis sp.*	Bedding* reported in Lenz (2005)* and Gouge (2005)*	F-tree trunk	Injection of nematodes in trunk	Control incomplete	Negative	Negative	
Hodotermitidae								
Anacanthotermes ahngerianus	*Steinernema carpocapsae*	Stadykov et al. (1973)	L-Petri dish	Contact / inoculated filter paper	High mortality	Positive	Inconclusive	P
Termopsidae								
Zootermopsis angusticollis	*Steinernema carpocapsae*	Wilson-Rich et al. (2007)	L-Petri dish	Contact / inoculated filter paper	Mortality is dose-dependent	Inconclusive	Inconclusive	
Zootermopsis sp.	*Steinernema carpocapsae*	Georgis et al. (1982), also reported in Anonymous (1982a)*	L-Petri dish	Contact / inoculated filter paper	96% mortality in 3d	Positive	Inconclusive	P
Zootermopsis sp.	*Steinernema sp.*	Samarasinghe (1994)	L-Petri dish	Contact / inoculated filter paper	Low mortality	Negative	Negative	
Kalotermitidae								
Glyptotermes dilatatus	*Heterorhabditis sp.*	Dantharanarayana and Vitharana (1987), also reported in Vitharana (1988)	F-Bush stem	Injection of nematodes in bush stems	High mortality at high dosage within 2-3mo, but only as a mycoinsecticide approach	Positive	Positive	
Neotermes rainbowi	*Heterorhabditis sp.*	Lenz and Runko (1992)*	L-Container	Various bedding	High mortality at high dosage	Positive	Positive	
Neotermes rainbowi	*Heterorhabditis sp.*	Lenz and Runko (1992)*	F-Tree cavity	Injection in coconut tree cavity	High dosage required to kill a colony	Positive	Positive	
Neotermes sp.	*Heterorhabditis indicus*	Lenz et al. (2000)*	F-Tree cavity	Injection in mahogany tree	Reduction of termite activity, but termites can refuge in individual branches	Inconclusive	Inconclusive	
Neotermes sp.	*Heterorhabditis sp.*	Lenz and Runko (1995)*	F-Tree cavity	Injection in tree trunk	64% of colonies were controlled	Inconclusive	Inconclusive	
Postelectrotermes militaris	*Heterorhabditis sp.*	Amarasinghe and Hominick (1993a)	L-Bush Stem	Injection of in lab stems cavities	High mortality at medium dosage	Positive	Positive	
Postelectrotermes militaris	*Steinernema carpocapsae*	Amarasinghe and Hominick (1993a)	L-Bush Stem	Injection of in lab stems cavities	High mortality at high dosage	Positive	Positive	
Postelectrotermes militaris	*Steinernema carpocapsae*	Amarasinghe and Hominick (1993b)	F-Tree cavity	Injection in bush stem cavities	Low to medium mortality	Inconclusive	Inconclusive	
Postelectrotermes militaris	*Steinernema feltiae*	Amarasinghe and Hominick (1993b)	F-Tree cavity	Injection in bush stem cavities	Low to medium mortality	Inconclusive	Inconclusive	
Rhinotermitidae								
Subterranean sp.	Not specified	Reported in Olkowski et al. (1991)*	F-PMP reports	Soil treatment from Pest control operators	Mortality observed	Positive	Inconclusive	N, V
Subterranean sp.	Not specified	Reported in Hall (1986)*	F-PMP reports	Soil treatment from Pest control operators	Mortality observed	Positive	Inconclusive	N, V
Coptotermes formosanus	*Heterorhabditis bacteriophora*	Wang et al. (2002b)	L-Petri dish	Contact / inoculated filter paper	High mortality at high dosage	Inconclusive	Inconclusive	
Coptotermes formosanus	*Heterorhabditis indica*	Wang et al. (2002b)	L-Petri dish	Contact / inoculated filter paper	High mortality at high dosage	Inconclusive	Inconclusive	
Coptotermes formosanus	*Heterorhabditis indica*	Mankowski et al. (2005)	L-Petri dish	Contact / inoculated filter paper	Medium mortality at high dosage, but grooming reduce the mortality	Negative	Negative	
Coptotermes formosanus	*Rhabditis rainai*	Coppel and Liang (1987)*, Carta and Osbrink (2005)	L-Petri dish	Unknown	Low mortality (30%)	Negative	Negative	

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Coptotermes formosanus	*Steinernema carpocapsae*	Fujii (1975)*, also reported in Tamashiro (1976)*	L-Petri dish	Contact / inoculated filter paper	High mortality at high dosage in 7d	Inconclusive	Inconclusive	
Coptotermes formosanus	*Steinernema carpocapsae*	Wang et al. (2002b)	L-Petri dish	Contact / inoculated filter paper	Medium mortality at high dosage	Inconclusive	Inconclusive	
Coptotermes formosanus	*Steinernema carpocapsae*	Mankowski et al. (2005)	L-Petri dish	Contact / inoculated filter paper	Medium mortality at high dosage, grooming reduce the mortality	Negative	Negative	
Coptotermes formosanus	*Steinernema feltiae*	Tamashiro (1976)*, also reported in Reese (1971)*	F- Bait traps	Unknown. Tamashiro preliminary test.	Low efficacy	Negative	Negative	
Coptotermes formosanus	*Steinernema feltiae*	Anonymous (1982b)	L-Petri dish	Contact / inoculated filter paper	Low mortality	Negative	Negative	
Coptotermes formosanus	*Steinernema feltiae*	Wu et al. (1991)	L-Petri dish	Contact / inoculated filter paper	High mortality in 6d	Positive	Inconclusive	P
Coptotermes formosanus	*Steinernema feltiae*	Wu et al. (1991)	L-Jar/soil	Contact / inoculated soil layer	High mortality at high dosage in 7d but repellency observed	Positive	Inconclusive	P, C
Coptotermes formosanus	*Steinernema riobrave*	Wang et al. (2002b)	L-Petri dish	Contact / inoculated filter paper	Medium mortality at high dosage	Inconclusive	Inconclusive	
Coptotermes gestroi	*Heterorhabditis indica*	Mankowski et al. (2005)	L-Petri dish	Contact / inoculated filter paper	Low mortality at high dosage, grooming reduce the mortality	Negative	Negative	
Coptotermes gestroi	*Steinernema carpocapsae*	Mankowski et al. (2005)	L-Petri dish	Contact / inoculated filter paper	Low mortality at high dosage, grooming reduce the mortality	Negative	Negative	
Coptotermes sp.	*Heterorhabditis sp.*	Bedding*, reported in Watson (1990)*	L	Unknown	Low mortality	Negative	Negative	
Coptotermes sp.	*Heterorhabditis sp.*	Bedding*, reported in Lenz (2005)*	F	Contact/ isolated population	The isolated population died	Inconclusive	Inconclusive	
Heterotermes aureus	*Heterorhabditis bacteriophora*	Weeks and Baker (2004)*	L-Containers	Contact / inoculated soil layer	Low mortality	Negative	Negative	
Heterotermes aureus	*Heterorhabditis bacteriophora*	Yu et al. (2006) and Yu et al. (2008)	L-Petri dish	Contact / inoculated sand layer	Low mortality	Negative	Negative	
Heterotermes aureus	*Steinernema carpocapsae*	Weeks and Baker (2004)*	L-Containers	Contact / inoculated soil layer	High mortality and no repellency observed	Positive	Inconclusive	P
Heterotermes aureus	*Steinernema carpocapsae*	Yu et al. (2006) and Yu et al. (2008)	L-Petri dish	Contact / inoculated sand layer	Medium mortality	Positive	Inconclusive	P
Heterotermes aureus	*Steinernema feltiae*	Yu et al. (2006) and Yu et al. (2008)	L-Petri dish	Contact / inoculated sand layer	Low mortality	Negative	Negative	
Heterotermes aureus	*Steinernema riobrave*	Yu et al. (2006) and Yu et al. (2008)	L-Petri dish	Contact / inoculated sand layer	High mortality	Positive	Inconclusive	P
Heterotermes tenuis	*Steinernema carpocapsae*	Passos and Alves, (1995)*, reported in Grewald et al. (2001)	L-Petri dish	Contact	High mortality observed	Positive	Inconclusive	P, N
Heterotermes tenuis	*Steinernema carpocapsae*	Alves*, reported in Grewal et al. (2001) and Yu et al. (2006)	L-Petri dish	Contact / corrugated cardboard	High mortality observed	Positive	Inconclusive	P, N
Psammotermes hybostoma	*Heterorhabditis bacteriophora*	Ibrahim and Abd El-Latif (2008)*	L-Containers	Contact / inoculated filter paper	High mortality at high dosage	Positive	Inconclusive	P, C
Psammotermes hybostoma	*Steinernema carpocapsae*	Ibrahim and Abd El-Latif (2008)*	L-Containers	Contact / inoculated filter paper	High mortality at high dosage	Positive	Inconclusive	P, C
Reticulitermes flavipes	*Heterorhabditis bacteriophora*	Mauldin and Beal (1989)	L-Lab colony	Contact / inoculated soil layer	Termites avoidance, low mortality	Negative	Negative	
Reticulitermes flavipes	*Heterorhabditis bacteriophora*	Mauldin and Beal (1989) also reported in Anonymous (1985b)*, Mix (1985, 1986)*	F-wood logs	Injection in the infested wood logs	Absence of termite control	Negative	Negative	
Reticulitermes flavipes	*Heterorhabditis bacteriophora*	Wang et al. (2002b)	L-Petri dish	Contact / inoculated filter paper	Medium mortality at high dosage	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Heterorhabditis bacteriophora*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	Low mortality	Inconclusive	Negative	N
Reticulitermes flavipes	*Heterorhabditis heliothidis*	Trudeau (1989)*	L-Petri dish	Contact / inoculated filter paper	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Heterorhabditis indica*	Wang et al. (2002b)	L-Petri dish	Contact / inoculated filter paper	High mortality at high dosage	Inconclusive	Inconclusive	

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Reticulitermes flavipes	*Heterorhabditis sp.*	Samarasinghe (1994)	L-Petri dish	Contact / inoculated filter paper	Medium mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Neosteinernema longicurvicauda*	Nguyen and Smart (1994)	L-Petri dish	Contact / corrugated cardboard	Sp. description, termite pathogen	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Rhabditis sp.*	Wang et al. (2002c)	L-Petri dish	Sand, vermiculite and cardboard	Natural occurrence of nematodes in termites	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Steinernema bibionis*	Trudeau (1989)*	L-Petri dish	Contact / inoculated filter paper	No mortality	Negative	Negative	
Reticulitermes flavipes	*Steinernema carpocapsae*	Wang et al. (2002b)	L-Petri dish	Contact / inoculated filter paper	Medium mortality at high dosage	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Steinernema carpocapsae*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	Medium mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Steinernema feltiae*	Trudeau (1989)*	L-Petri dish	Contact / inoculated filter paper	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Steinernema feltiae*	Mauldin and Beal (1989)	L-Lab colony	Contact / inoculated soil layer	Termites avoidance, low mortality	Negative	Negative	
Reticulitermes flavipes	*Steinernema feltiae*	Mauldin and Beal (1989) also reported in Anonymous (1985b)*, Mix (1985)*, Mix (1986)*	F-wood logs	Injection in the infested wood logs	Absence of termite control	Negative	Negative	
Reticulitermes flavipes	*Steinernema feltiae*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	Low mortality	Negative	Negative	
Reticulitermes flavipes	*Steinernema glaseri*	Trudeau (1989)*	L-Petri dish	Contact / inoculated filter paper	No mortality	Negative	Negative	
Reticulitermes flavipes	*Steinernema riobrave*	Wang et al. (2002b)	L-Petri dish	Contact / inoculated filter paper	No mortality at high dosage	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Steinernema riobrave*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	Low mortality	Negative	Negative	
Reticulitermes flavipes	*Steinernema sp.*	Samarasinghe (1994)	L-Petri dish	Contact / inoculated filter paper	High mortality at high concentration	Positive	Inconclusive	P, C
Reticulitermes hesperus	*Heterorhabditis bacteriophora*	Reported in Poinar and Georgis (1989)*	L-Petri dish	Contact / inoculated filter paper	Medium mortality	Inconclusive	Inconclusive	
Reticulitermes hesperus	*Steinernema carpocapsae*	Reported in Poinar and Georgis (1989)*	L-Petri dish	Contact / inoculated filter paper	High mortality	Positive	Inconclusive	P
Reticulitermes speratus	*Steinernema feltiae*	Wu et al. (1991)	L-Petri dish	Contact / inoculated filter paper	High mortality in 6d	Positive	Inconclusive	P
Reticulitermes speratus	*Steinernema feltiae*	Wu et al. (1991)	L-Jar/soil	Contact / inoculated soil layer	High mortality at high dosage in 7d	Positive	Inconclusive	P, C
Reticulitermes tibialis	*Steinernema feltiae*	Epsky and Capinera (1988)	L-Petri dish	Contact / inoculated filter paper	High mortality at high dosage	Positive	Inconclusive	P, C
Reticulitermes tibialis	*Steinernema feltiae*	Epsky and Capinera (1988)	F- bait traps	Contact / inoculated soil layer	Termites avoided treated soil	Negative	Negative	
Reticulitermes virginicus	*Heterorhabditis bacteriophora*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	No mortality	Negative	Negative	
Reticulitermes virginicus	*Steinernema carpocapsae*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	No mortality	Negative	Negative	
Reticulitermes virginicus	*Steinernema feltiae*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	Low mortality	Negative	Negative	
Reticulitermes virginicus	*Steinernema riobrave*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	Low mortality	Negative	Negative	
Reticulitermes sp.	*Steinernema carpocapsae*	Georgis et al. (1982)	L-Petri dish	Contact / inoculated filter paper	98% mortality in 3d	Positive	Inconclusive	P
Reticulitermes sp.	*Steinernema carpocapsae*	Anonymous (1985a)*	F-PMP reports	Saf-T-Shield™ termiticide injection into galleries	Some PMP claimed they killed some colonies.	Positive	Inconclusive	N
Reticulitermes sp.	*Steinernema sp.*	Anonymous (1983)*	F-Houses	Spear™ termiticide injection into galleries	Some PMP claimed they killed some colonies.	Positive	Inconclusive	N
Termitidae								
Ancistrotermes guineensis	*Heterorhabditis bacteriophora*	Rouland et al. (1996)	L-Petri dish	Contact / inoculated soil layer	High mortality in reproductives	Inconclusive	Inconclusive	
Ancistrotermes guineensis	*Steinernema carpocapsae*	Rouland et al. (1996)	L-Petri dish	Contact / inoculated soil layer	High mortality in reproductives	Inconclusive	Inconclusive	
Ancistrotermes guineensis	*Steinernema carpocapsae*	Benmoussa-Haichour et al. (1998)	L-Petri dish	Contact / inoculated soil layer	High mortality in 15d, nematodes do not complete their life cycle	Negative	Negative	
Ancistrotermes guineensis	*Steinernema kushidai*	Rouland et al. (1996)	L-Petri dish	Contact / inoculated soil layer	High mortality in reproductives	Inconclusive	Inconclusive	
Ancistrotermes guineensis	*Steinernema kushidai*	Benmoussa-Haichour et al. (1998)	L-Petri dish	Contact / inoculated soil layer	High mortality in 10d, nematodes do not complete their life cycle	Negative	Negative	
Cornitermes cumulans	*Steinernema carpocapsae*	Souza (2006)* reported in Rosa et al. (2008)*	L-Petri dish	Contact	High mortality	Positive	Inconclusive	P

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Cornitermes cumulans	*Steinernema carpocapsae*	Rosa et al. (2007)*	L-Petri dish	Contact, multiple strains tested	High mortality	Positive	Inconclusive	P
Cornitermes cumulans	*Steinernema carpocapsae*	Rosa et al. (2008)*	L-Petri dish	Contact	High mortality	Positive	Inconclusive	P
Gnathamitermes perplexus	*Heterorhabditis bacteriophora*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	No mortality	Negative	Negative	
Gnathamitermes perplexus	*Steinernema carpocapsae*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	High mortality	Positive	Inconclusive	P
Gnathamitermes perplexus	*Steinernema feltiae*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	Low mortality	Negative	Negative	
Gnathamitermes perplexus	*Steinernema riobrave*	Yu et al. (2006)	L-Petri dish	Contact / inoculated sand layer	High mortality	Positive	Inconclusive	P
Macrotermes Bellicosus	*Steinernema carpocapsae*	Benmoussa-Haichour et al. (1998)	L-Petri dish	Contact / inoculated soil layer	High mortality in 2-3d, nematodes do not complete their life cycle	Negative	Negative	
Macrotermes Bellicosus	*Steinernema kushidai*	Benmoussa-Haichour et al. (1998)	L-Petri dish	Contact / inoculated soil layer	High mortality in 3-4d, nematodes do not complete their life cycle	Negative	Negative	
Microcerotermes championi	Not specified	Khan et al. (1994)	L-Petri dish	Contact / inoculated filter paper	High mortality in 7d	Positive	Inconclusive	P
Nasutitermes corniger	*Steinernema carpocapsae*	Laumond et al. (1979)	L-Petri dish	Contact / inoculated filter paper	High mortality at high dosage	Positive	Inconclusive	P, C
Nasutitermes sp.	*Heterorhabditis sp.*	Bedding*, reported in Watson (1990)*	L	Unknown	Low mortality	Negative	Negative	
Odontotermes formosanus	*Steinernema carpocapsae*	Anonymous (1982b)	L-Petri dish	Contact / inoculated filter paper	High mortality	Positive	Inconclusive	P
Odontotermes formosanus	*Steinernema feltiae*	Anonymous (1982b)	L-Petri dish	Contact / inoculated filter paper	High mortality	Positive	Inconclusive	P
Odontotermes redemanni	*Steinernema feltiae*	Narayanan and Gopalakrishnan (1988)*	L-Petri dish	Contact / inoculated filter paper	High mortality even at low dosage	Positive	Inconclusive	P
Pseudacanthotermes spiniger	*Heterorhabditis bacteriophora*	Rouland et al. (1996)	L-Petri dish	Contact / inoculated soil layer	High mortality in reproductives	Inconclusive	Inconclusive	
Pseudacanthotermes spiniger	*Heterorhabditis bacteriophora*	Benmoussa-Haichour et al. (1998)	L-Petri dish	Contact / inoculated soil layer	High mortality in 10-20d, nematodes do not complete their life cycle	Negative	Negative	
Pseudacanthotermes Spiniger	*Steinernema carpocapsae*	Rouland et al. (1996)	L-Petri dish	Contact / inoculated soil layer	High mortality in reproductives	Inconclusive	Inconclusive	
Pseudacanthotermes Spiniger	*Steinernema carpocapsae*	Benmoussa-Haichour et al. (1998)	L-Petri dish	Contact / inoculated soil layer	Nematodes do not complete their life cycle	Negative	Negative	
Pseudacanthotermes Spiniger	*Steinernema kushidai*	Rouland et al. (1996)	L-Petri dish	Contact / inoculated soil layer	High mortality in reproductives	Inconclusive	Inconclusive	

[a]L= Lab, F= Field

[b]Explanation for disagreeing with the authors' interpretation. P=The experiment was performed in a Petri dish or equivalent, with poor biological relevancy to the given termite species and remains a screening test. C=Mortality was observed only with high concentrations of the pathogen which cannot be applied in the field. N=No data were provided to support the claim. V=The variability in the results shows that control was not consistent.

*Non-peer reviewed journal

Table 4a. Number of experiments testing 1 termite *sp.* against 1 fungal *sp.*, reported in the literature, peer reviewed and non-peer reviewed.

Fungi (152 reports, 280 experiments)	Laboratory tests[a,b]			Field tests[c]			Total
	Positive	Inconclusive	Negative	Positive	Inconclusive	Negative	
Authors' interpretation							
Peer reviewed	97	51	23	12	7	0	190
Non-peer reviewed	38	19	1	11	6	10	90
Total	135	70	24	28	13	10	280
Our re-interpretation							
Peer reviewed	21	127	23	7	12	0	190
Non-peer reviewed	2	55	1	2	19	11	90
Total	23	182	24	9	31	11	280

[a]Laboratory test = 229 experiments
[b]Petri dish = 206 experiments
[c]Field test = 51 experiments

Table 4b. Listing of experiments testing 1 termite *sp.* against 1 fungal *sp.*, reported in the literature.

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Mastotermitidae								
Mastotermes darwiniensis	*Metarhizium anisopliae*	Chouvenc et al. (2009)	L-Petri dish	Direct contact	No mortality even at high dosage	Negative	Negative	
Hodotermitidae								
Anacanthotermes ahngerianus	*Beauveria bassiana*	Vypiyach (1972)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Anacanthotermes ahngerianus	*Beauveria bassiana*	Lutikova (1990)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Anacanthotermes ahngerianus	*Beauveria bassiana*	Lutikova (1990)*	F	Injection around the nest	Nest material inhibited the fungus	Negative	Negative	
Hodotermes mossambicus	*Beauveria bassiana*	Gouse*, reported in Langewald et al. (2003)*	L- Petri dish	Unknown	High mortality at 6 d.	Positive	Inconclusive	P, N
Hodotermes mossambicus	*Beauveria bassiana*	Gouse*, reported in Langewald et al. (2003)*	F	Unknown	No successful epizootic	Negative	Negative	
Hodotermes mossambicus	*Metarhizium anisopliae*	Gouse*, reported in Langewald et al. (2003)*	L- Petri dish	Unknown	Low mortality to local strains but high mortality with imported strain.	Inconclusive	Inconclusive	
Hodotermes mossambicus	*Metarhizium anisopliae*	Gouse*, reported in Langewald et al. (2003)*	F	Unknown	No successful control	Negative	Negative	
Hodotermes mossambicus	*Metarhizium anisopliae*	Chouvenc et al. (2009)	L-Petri dish	Direct contact	High mortality at low dosage	Inconclusive	Inconclusive	
Termopsidae								
Hodotermopsis sjoestedti	*Metarhizium anisopliae*	Chouvenc et al. (2009)	L-Petri dish	Direct contact	Moderate mortality at high dosage	Negative	Negative	
Zootermopsis angusticollis	*Metarhizium anisopliae*	Rosengaus and Traniello (1997)	L-Petri dish	Direct contact	High mortality at high dosage	Inconclusive	Inconclusive	
Zootermopsis angusticollis	*Metarhizium anisopliae*	Rosengaus et al. (1998)	L-Petri dish	Direct contact	Lower mortality when termites are in larger groups	Negative	Negative	
Zootermopsis sp.	*Beauveria bassiana*	Samarasinghe (1994)	L-Petri dish	Direct contact/ Feeding	Low mortality	Negative	Negative	
Zootermopsis sp.	*Metarhizium anisopliae*	Samarasinghe (1994)	L-Petri dish	Direct contact/ Feeding	High mortality	Positive	Inconclusive	P
Kalotermitidae								
Cryptotermes brevis	*Metarhizium anisopliae*	Leong (1966)*	L-Petri dish	Direct contact	High mortality, but no fungal development	Inconclusive	Inconclusive	
Cryptotermes brevis	*Metarhizium anisopliae*	Kaschef and Abou-Zeid (1987)*	L-Petri dish	Direct contact	50% mortality in 5 d	Inconclusive	Inconclusive	
Cryptotermes brevis	*Metarhizium anisopliae*	Nasr and Moein (1997)	L-Petri dish	Feeding on filter paper and wood	High mortality at high dosage	Positive	Positive	
Cryptotermes brevis	*Verticillium indicum*	Nasr and Moein (1997)	L-Petri dish	Feeding on filter paper and wood	High mortality at high dosage	Positive	Positive	
Cryptotermes cynocephalus	*Metarhizium anisopliae*	Sukartana*, reported in Sukartana et al. (2000)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P, N
Glyptotermes dilatatus	*Metarhizium anisopliae*	Vitharana (1988)	F-Bush stem	Injection of conidia in bush stems	Mortality with a mycoinsecticide approach	Positive	Positive	
Kalotermes flavicollis	*Metarhizium anisopliae*	Chouvenc et al. (2009)	L-Petri dish	Direct contact	High mortality at low dosage	Inconclusive	Inconclusive	
Incistitermes immigrans	*Metarhizium anisopliae*	Leong (1966)*	L-Petri dish	Direct contact	High mortality, but no sporulation	Inconclusive	Inconclusive	
Neotermes connexus	*Metarhizium anisopliae*	Leong (1966)*	L-Petri dish	Direct contact	Medium mortality and sporulation	Inconclusive	Inconclusive	
Neotermes rainbowi	*Metarhizium anisopliae*	Lenz and Runko (1992)*	F- Tree	Application to tree trunk	Colony eradicated	Positive	Positive	
Neotermes sp.	*Metarhizium anisopliae*	Lenz and Runko (1995)*	F- Tree	Application to tree trunk	94% of colonies killed	Positive	Positive	
Neotermes sp.	*Metarhizium anisopliae*	Lenz et al. (2000)*	F- Tree	Injection in mahogany tree	Reduction of termite activity	Positive	Inconclusive	V

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Rhinotermitidae								
Coptotermes acinaciformis	*Metarhizium anisopliae*	Milner (1991)*, also reported in Anonymous, (1991)*	L- Petri dish	Direct contact	High mortality	Positive	Positive	
Coptotermes acinaciformis	*Metarhizium anisopliae*	Rath and Tidbury (1996)	L-Petri dish	Direct contact, high concentration	High mortality	Positive	Positive	
Coptotermes acinaciformis	*Metarhizium anisopliae*	Milner et al. (1998a)	L-Petri dish	Direct contact, strain selection	High mortality	Positive	Positive	
Coptotermes acinaciformis	*Metarhizium anisopliae*	Milner and Staples (1996), also reported in Milner et al. (1996)*	F-mound	Pure conidia blown in the nest	Colony can be destroyed with large amount of conidia, but remain inconclusive	Inconclusive	Inconclusive	
Coptotermes acinaciformis	*Metarhizium anisopliae*	Milner et al. (1997a)	L-Petri dish	Direct contact, humidity selection	High mortality, 93% RH needed for sporulation	Positive	Positive	
Coptotermes acinaciformis	*Metarhizium anisopliae*	Staples and Milner (2000b)*	F-Houses	Direct application in infested wood	Some mortality observed	Inconclusive	Inconclusive	
Coptotermes curvignathus	*Conidiobolus coronatus*	Sajap et al. (1997)	L-Petri dish	Direct contact, high dosage	High mortality	Positive	Inconclusive	P, C
Coptotermes curvignathus	*Conidiobolus villosus*	Aziz (1977)*	F-Tree base	Unknown	Ineffective against field colonies	Negative	Negative	
Coptotermes curvignathus	*Conidiobolus sp.*	Altson (1947)	L-Petri dish	Direct contact/ feeding	High mortality	Positive	Inconclusive	P
Coptotermes curvignathus	*Metarhizium anisopliae*	Sajap and Kaur (1990)	L-Petri dish	Direct contact, Histology	Pathogenic	Inconclusive	Inconclusive	
Coptotermes curvignathus	*Metarhizium anisopliae*	Hoe et al. (2009)	L-Petri dish	Direct contact	High mortality at high dosage	Positive	Inconclusive	P, C
Coptotermes frenchi	*Metarhizium anisopliae*	Milner et al., (1998a)	L-Petri dish	Direct contact, strain selection	High mortality	Positive	Positive	
Coptotermes frenchi	*Metarhizium anisopliae*	Milner and Staples (1996), also reported in Milner et al. (1996)*	F-mound	Pure conidia blown in the nest	Colony can be destroyed with large amount of conidia, but remain inconclusive	Inconclusive	Inconclusive	
Coptotermes formosanus	*Aspergillus flavus*	Jayasimha and Henderson (2007)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Aspergillus fumigatus*	Chai et al. (1995)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Aspergillus niger*	Suzuki (1991, 1995)*	L-Petri dish	Direct contact/ Feeding	Medium mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Basidiobolus sp.*	Krejzová (1972)	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Coptotermes formosanus	*Beauveria bassiana*	Leong (1966)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Beauveria bassiana*	Tamashiro (1968)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Beauveria bassiana*	Lai (1977)*, also reported in Tamashiro (1976)*	F-Colony	Trap, treat release	No epizootic	Negative	Negative	
Coptotermes formosanus	*Beauveria bassiana*	Lai et al. (1982)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Beauveria bassiana*	Delate et al. (1995), also reported in Grace (1995)*	L-Vials Choice test	Bait and refuge, distances involved	High mortality	Positive	Positive	
Coptotermes formosanus	*Beauveria bassiana*	Suzuki (1991, 1995)*	L-Petri dish	Direct contact/ Feeding	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Beauveria bassiana*	Suzuki (1991, 1995)*	F-Tree	Tree trunk coated with fungus	Partial mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Beauveria bassiana*	Wells et al. (1995)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Beauveria bassiana*	Jones et al. (1996) also reported in Grace (1991, 1993,1995)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Beauveria bassiana*	Wright et al. (2002)	L-Petri dish	Direct contact and transfer	High mortality but strain dependent	Inconclusive	Inconclusive	
Coptotermes formosanus	*Beauveria bassiana*	Sun et al. (2002)	L-Petri dish	Direct contact, sporulation patern	Pathogenic but slow sporulation	Inconclusive	Inconclusive	
Coptotermes formosanus	*Beauveria bassiana*	Sun et al. (2003a)	L-Chambers	Direct contact and transfer	Partial transfer and mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Beauveria bassiana*	Sun et al. (2003b)	L-Petri dish	Direct contact	Medium mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Beauveria bassiana*	Wang and Powell (2003)	L-Petri dish	Direct contact	Medium mortality	Inconclusive	Inconclusive	

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Coptotermes formosanus	*Beauveria bassiana*	Hussain et al. (2010)	L-Container	Direct contact/ olfaction bioassay	Medium mortality and medium avoidance	inconclusive	Inconclusive	
Coptotermes formosanus	*Beauveria brongniartii*	Yoshimura and Takahashi (1998)	L-Petri dish	Direct contact and transfer	High mortality at high dosage and at high ratio infected/naïve termites	Positive	Inconclusive	P, C
Coptotermes formosanus	*Beauveria brongniartii*	Yanagawa et al. (2008)	L-Petri dish	Direct contact	High mortality at high dosage, grooming	Inconclusive	Inconclusive	
Coptotermes formosanus	*Conidiobolus coronatus*	Tamashiro (1968)*	L-Petri dish	Direct contact	Medium mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Conidiobolus coronatus*	Krejzová (1975)	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Conidiobolus coronatus*	Krejzová (1977)	L-Petri dish	Direct contact, fungus reisolation	High mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Conidiobolus coronatus*	Ko et al. (1982)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Conidiobolus coronatus*	Yoshimura et al. (1992)	L-Petri dish	Direct contact and transfer	High mortality, transfer depends on group size	Positive	Inconclusive	P
Coptotermes formosanus	*Conidiobolus coronatus*	Wells et al. (1995)	L-Petri dish	Direct contact	Indirect mortality and no sporulation	Negative	Negative	
Coptotermes formosanus	*Entomophthora destruens*	Krejzová (1972)	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Entomophthora sp.*	Krejzová (1971)	L-Petri dish	Direct contact, various spp.	High mortality to *E. thaxteriana*	Inconclusive	Inconclusive	
Coptotermes formosanus	*Isaria cicadae*	Chai et al. (1995)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Isaria fumosorosea*	Krejzová (1976)	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Coptotermes formosanus	*Isaria fumosorosea*	Chai et al. (1995)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Isaria fumosorosea*	Suzuki (1991, 1995)*	L-Petri dish	Direct contact/ Feeding	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Isaria fumosorosea*	Suzuki (1991, 1995)*	F-Tree	Tree trunk coated with fungi	Presence of termites after 3yr	Negative	Negative	
Coptotermes formosanus	*Isaria fumosorosea*	Meikle et al. (2005)	L-Petri dish	Container	High mortality even when in large groups	Positive	Inconclusive	P, C
Coptotermes formosanus	*Isaria fumosorosea*	Dunlap et al. (2007)	L-Petri dish	Foam formulation test	High mortality	Positive	Inconclusive	P, C
Coptotermes formosanus	*Isaria fumosorosea*	Yanagawa et al. (2008)	L-Petri dish	Direct contact	High mortality at high dosage, grooming	Inconclusive	Inconclusive	
Coptotermes formosanus	*Isaria fumosorosea*	Hussain et al. (2010)	L-Container	Direct contact/ olfaction bioassay	High mortality and low avoidance	Positive	Inconclusive	P, C
Coptotermes formosanus	*Metarhizium anisopliae*	Leong (1966)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Tamashiro (1968)*, also reported in Reese (1971)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Lai (1977)*, also reported in Tamashiro (1976)*	F-Colony	Trap, treat release	No epizootic	Negative	Negative	
Coptotermes formosanus	*Metarhizium anisopliae*	Ko et al. (1982)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Lai et al. (1982)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Chai et al. (1995)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Delate et al. (1995), also reported in Grace (1995)*	L-Choice test	Bait and refuge, short distances	High mortality	Positive	Positive	
Coptotermes formosanus	*Metarhizium anisopliae*	Rath (1995)*	F	Drill and treat application	Low re-infestation after 2 yr	Positive	Inconclusive	N, V
Coptotermes formosanus	*Metarhizium anisopliae*	Suzuki (1991, 1995)*	L-Petri dish	Direct contact/ Feeding	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Suzuki (1991, 1995)*	F-Tree	Tree trunk coated with fungi	Presence of termites after 3yr	Negative	Negative	
Coptotermes formosanus	*Metarhizium anisopliae*	Wells et al. (1995)	L-Petri dish	Direct contact	High morality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Jones et al. (1996) also reported in Grace (1991, 1993)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Sun et al. (2002)	L-Petri dish	Direct contact, sporulation pattern	Pathogenic and fast sporulation	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Wright et al. (2002)	L-Petri dish	Direct contact and transfer	High mortality but strain dependent	Inconclusive	Inconclusive	

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Coptotermes formosanus	*Metarhizium anisopliae*	Sun et al. (2003a)	L-Chambers	Direct contact and transfer	Partial transfer and mortality	Positive	Inconclusive	V
Coptotermes formosanus	*Metarhizium anisopliae*	Sun et al. (2003b)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Engler and Gold (2004)	L-Test tubes	Direct contact	Low mortality, attractant	Inconclusive	Inconclusive	
Coptotermes formosanus	*Metarhizium anisopliae*	Huang (2004)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P, C
Coptotermes formosanus	*Metarhizium anisopliae*	Huang (2004)*	F-Roots	Roots of young *Eucalyptus*	Reduced termite damage on young tree, no data on termite control	Positive	Inconslusive	N, V
Coptotermes formosanus	*Metarhizium anisopliae*	Wang and Powell (2004)	L-Container	Sand/vermiculite, cellulose bait	Mortality at high dosage, some repellency	Positive	Inconclusive	C
Coptotermes formosanus	*Metarhizium anisopliae*	Meikle et al. (2005)	L-Container	Container	Low mortality when in large groups	Negative	Negative	
Coptotermes formosanus	*Metarhizium anisopliae*	Wright et al. (2005)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes formosanus	*Metarhizium anisopliae*	Sun et al. (2008)	L-Arena	Foraging on treated mulch	Mortality and repellency	Positive	Inconclusive	V
Coptotermes formosanus	*Metarhizium anisopliae*	Yanagawa et al. (2008)	L-Petri dish	Direct contact	High mortality at high dosage, grooming	Inconclusive	Inconclusive	
Coptotermes formosanus	*Metarhizium anisopliae*	Liao et al. (2009)*	F-Seed	Coated *Eucalyptus* seed	Reduced termite damage on young tree, no data on termite control	Positive	Inconclusive	N, V
Coptotermes formosanus	*Metarhizium anisopliae*	Hussain et al. (2010)	L-Container	Direct contact/ olfaction bioassay	Low mortality because of avoidance	Inconclusive	Inconclusive	
Coptotermes formosanus	*Metarhizium flavoviride*	Wells et al. (1995)	L-Petri dish	Direct contact	Low virulence	Negative	Negative	
Coptotermes gestroi	*Beauveria bassiana*	Tamashiro (1968)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes gestroi	*Conidiobolus coronatus*	Tamashiro (1968)*	L-Petri dish	Direct contact	Medium mortality	Inconclusive	Inconclusive	
Coptotermes gestroi	*Metarhizium anisopliae*	Tamashiro (1968)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes gestroi	*Metarhizium anisopliae*	Sukartana et al. (2000)*	L-Petri dish	Direct contact, unknown concentrations	High mortality	Positive	Inconclusive	P, C, N
Coptotermes gestroi	*Metarhizium anisopliae*	Maketon et al. (2007)	L-Petri dish	Direct contact/ Feeding	High mortality at high dosage	Positive	Inconclusive	P, C
Coptotermes heimi	*Metarhizium anisopliae*	Ahmed et al. (2008a)	L-Petri dish	Direct contact, various strains	Various mortality rate	Positive	Inconclusive	P, V
Coptotermes heimi	*Metarhizium anisopliae*	Ahmed et al. (2008b)	L-Petri dish	Direct contact, various strains	Various mortality rate	Positive	Inconclusive	P, V
Coptotermes heimi	*Metarhizium anisopliae*	Ahmed et al. (2009)	L-Petri dish	Direct contact, various strains	High mortality	Positive	Inconclusive	P
Coptotermes lacteus	*Beauveria bassiana*	Staples and Milner (2000a)	L-Tube	Foraging in tube/treated soil	Low mortality and low repellency	Negative	Negative	
Coptotermes lacteus	*Metarhizium anisopliae*	Staples and Milner (2000a)	L-Tube	Foraging in tube/treated soil	High mortality but high repellency	Positive	Inconclusive	V
Coptotermes lacteus	*Metarhizium anisopliae*	Staples and Milner (2000b)*	F-Houses	Direct application in infested wood	Partial mortality and repellency	Positive	Inconclusive	V
Coptotermes lacteus	*Metarhizium anisopliae*	Reported in Milner (2003)	F-Mound	Direct application in the nest	Partial mortality, High dosage required	Inconclusive	Inconclusive	
Coptotermes sp.	*Beauveria bassiana*	Kartika et al. (2006)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes sp.	*Metarhizium anisopliae*	Krutmuang and Mekchay, (2005)*, also reported in Krutmuang (1996)*	L-Petri dish	Direct contact/ Feeding	High mortality at high dosage	Positive	Inconclusive	P, C
Coptotermes sp.	*Metarhizium anisopliae*	Horwood et al. (2010)	F-Poles	Direct injection into infested electric poles.	Reduced infestation within a month but reinfestation after six months..	Inconclusive	Inconclusive	
Coptotermes sp.	*Metarhizium anisopliae*	Kartika et al. (2006)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Coptotermes sp.	*Humicola sp.*	Guswenrivo et al. (2007)*	L-Petri dish	Direct contact/ Feeding	High mortality at 14d	Positive	Inconclusive	P
Heterotermes tenuis	*Beauveria bassiana*	Almeida and Alves (1996)	L-Petri dish	Direct contact, in association with Imidacloprid	High mortality, synergy.	Positive	Inconclusive	P
Heterotermes tenuis	*Beauveria bassiana*	Almeida et al. (1997)	L-Petri dish	Direct contact, stain selection	High mortality, isolate 634 optimal	Positive	Inconclusive	P
Heterotermes tenuis	*Beauveria bassiana*	Almeida et al. (1998)	F-Baiting	Sugar can field, in association with Imidacloprid	Reduction of termite activity, but no data to support the non-repellency	Positive	Inconclusive	N, V
Heterotermes tenuis	*Beauveria bassiana*	Almeida and Alves (1999)	F-Baiting	Sugar can field, in association with Imidacloprid	Reduction of termite activity but no confirmation colony control	Positive	Inconclusive	N, V

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Heterotermes tenuis	*Beauveria bassiana*	Moino and Alves (1998)	L-Petri dish	In association with Imidacloprid	Reduction of grooming activity and increased mortality	Positive	Inconclusive	P
Heterotermes tenuis	*Beauveria bassiana*	Moino et al. (2002)	L-Petri dish	Direct contact, SEM preparation	Adhesion and penetration, death of the insects	Positive	Inconclusive	P, N
Heterotermes tenuis	*Beauveria brongniartii*	Almeida et al. (1997)	L-Petri dish	Direct contact, stain selection	Strains not optimal for mortality	Inconclusive	Inconclusive	
Heterotermes tenuis	*Metarhizium anisopliae*	Almeida et al. (1997)	L-Petri dish	Direct contact, stain selection	Strains not optimal for mortality	Inconclusive	Inconclusive	
Heterotermes tenuis	*Metarhizium anisopliae*	Moino and Alves (1998)	L-Petri dish	In association with Imidacloprid	Reduction of grooming activity and increased mortality	Positive	Inconclusive	P
Heterotermes tenuis	*Metarhizium anisopliae*	Moino et al. (2002)	L-Petri dish	Direct contact, SEM preparation	Adhesion and penetration, death of the insects	Positive	Inconclusive	P, N
Psammotermes hybostoma	*Beauveria bassiana*	Ezz and Abd El-Latif (2008a)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P, N
Psammotermes hybostoma	*Beauveria bassiana*	Ezz and Abd El-Latif (2008b)*	L-container	Use of infected cadavers	High mortality, transfer	Positive	Inconclusive	P, N
Prorhinotermes canalifrons	*Metarhizium anisopliae*	Chouvenc et al. (2009)	L-Petri dish	Direct contact	High mortality at high dosage	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Aspergillus flavus*	Lund (1965b)* also reported in Lund (1962)	L-Petri dish	Unknown	Rapid mortality	Positive	Inconclusive	P, N
Reticulitermes flavipes	*Aspergillus flavus*	Lund (1971)*	F	Unknown	No significant pathogenicity	Negative	Negative	
Reticulitermes flavipes	*Beauveria bassiana*	Toumanoff and Rombaut (1965)	L-Petri dish	Cellulose formulation	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Beauveria bassiana*	Bao and Yendol (1971)	L-Petri dish	Direct contact/ Histopathology	Adhesion and penetration, death of the insects	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Beauveria bassiana*	Zoberi and Grace (1990)	L-Petri dish	Direct contact	High mortality but avoidance of infected individual by healthy termite	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Beauveria bassiana*	Grace and Zoberi (1992)	L-Petri dish	Direct contact on part of the group	Larger group of treated termite needed to achieve high mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Beauveria bassiana*	Samarasinghe (1994)	L-Petri dish	Direct contact/ Feeding	Low mortality	Negative	Negative	
Reticulitermes flavipes	*Beauveria bassiana*	Boucias et al. (1996)	L-Petri dish	In association with Imidacloprid	Reduction of grooming activity and increased mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Beauveria bassiana*	Wang and Powell (2003)	L-Petri dish	Direct contact	Medium mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Beauveria sp.*	Toumanoff (1965)	L-Petri dish	Direct contact, various sp.	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Conidiobolus coronatus*	Yendol and Paschke (1965)	L-Petri dish	Direct contact/ Feeding	High mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Conidiobolus coronatus*	Yendol and Rosario (1972)	L-Petri dish	Direct contact, testing protocol	High mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Conidiobolus coronatus*	Zeck (1992)*	F	In association with Imidacloprid	High mortality, but no need for fungi	Positive	Inconclusive	N
Reticulitermes flavipes	*Entomophthora virulenta*	Yendol and Paschke (1965)	L-Petri dish	Direct contact/ Feeding	Low mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Entomophthora virulenta*	Page (1966)*	L-Petri dish	In combination with *Bacillus thuringiensis*	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Isaria sp.*	Toumanoff (1965)	L-Petri dish	Direct contact, various sp.	High mortality, depending on sp.	Positive	Inconclusive	P, V
Reticulitermes flavipes	*Isaria sp.*	Smythe and Coppel (1966)	L-Container	Direct contact	Low mortality when in groups	Negative	Negative	
Reticulitermes flavipes	*Metarhizium anisopliae*	Toumanoff (1965)	L-Petri dish	Direct contact, various sp.	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Metarhizium anisopliae*	Toumanoff and Rombaut (1965)	L-Petri dish	Cellulose formulation	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Metarhizium anisopliae*	Zeck (1992)*	L-Petri dish	In association with Imidacloprid	High mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Metarhizium anisopliae*	Zeck (1992)*	F-Baiting	In association with Imidacloprid	Reduction of termite activity	Positive	Inconclusive	N, V
Reticulitermes flavipes	*Metarhizium anisopliae*	Samarasinghe (1994)	L-Petri dish	Direct contact/ Feeding	High mortality, various strains	Positive	Inconclusive	P
Reticulitermes flavipes	*Metarhizium anisopliae*	Myles, reported in Quarles (1995)*	F-Colonies	Trap and treat, T. Myles assays (see Myles, 1996)	Confusion about various control techniques	Positive	Negative	N

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Reticulitermes flavipes	*Metarhizium anisopliae*	Rath (1995)*	F-Colonies	Drill and treat application	Low re-infestation after 2 yr	Positive	Inconclusive	V, N
Reticulitermes flavipes	*Metarhizium anisopliae*	Zoberi (1995)	L-Petri dish	Direct contact and transmission	High mortality, transmission occurred	Positive	Inconclusive	P
Reticulitermes flavipes	*Metarhizium anisopliae*	Ramakrishnan et al. (1999)	L-Petri dish	In association with Imidacloprid	Increased mortality	Positive	Inconclusive	P
Reticulitermes flavipes	*Metarhizium anisopliae*	Strack (2000)*	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Metarhizium anisopliae*	Strack (2000)*	L-Soil cups	Direct contact to a part of the colony	No transmission to the rest of the colony	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Metarhizium anisopliae*	Myles (2002)	L-Petri dish	Direct contact and transfer	Mortality and transfer, importance of dosing, repellency	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Metarhizium anisopliae*	Wang and Powell (2003)	L-Petri dish	Direct contact	High morality	Positive	Inconclusive	P
Reticulitermes flavipes	*Metarhizium anisopliae*	Engler and Gold (2004)	L-Test tubes	Direct contact	Low mortality, attractant	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Metarhizium anisopliae*	Engler and Gold (2004)	F-Stations	Bait stations	High termite activity	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Metarhizium anisopliae*	Wang and Powell (2004)	L-Container	Sand/vermiculite, cellulose bait	Mortality but repellency at lethal concentrations	Positive	Inconclusive	C
Reticulitermes flavipes	*Metarhizium anisopliae*	Chouvenc et al. (2008)	L-Arena	Direct contact, trap and treat	No epizootic observed	Negative	Negative	
Reticulitermes flavipes	*Metarhizium anisopliae*	Chouvenc et al. (2009)	L-Petri dish	Direct contact	High mortality at high dosage	Inconclusive	Inconclusive	
Reticulitermes flavipes	*Penicillium oxalicum*	Smythe and Coppel (1966)	L-Container	Direct contact	High mortality when in groups	Inconclusive	Inconclusive	
Reticulitermes grassei	*Beauveria bassiana*	Santiago-Alvarez et al. (2005)	L-Petri dish	Direct contact	High mortality at high dosage	Positive	Inconclusive	P, C
Reticulitermes grassei	*Metarhizium anisopliae*	Santiago-Alvarez et al. (2005)	L-Petri dish	Direct contact	High mortality at high dosage	Positive	Inconclusive	P, C
Reticulitermes lucifugus	*Basidiobolus sp.*	Krejzová (1972)	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Reticulitermes lucifugus	*Beauveria bassiana*	Vypiyach and Voronkina (1972)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Reticulitermes lucifugus	*Conidiobolus coronatus*	Krejzová (1975)	L-Petri dish	Direct contact	Medium mortality	Inconclusive	Inconclusive	
Reticulitermes lucifugus	*Conidiobolus coronatus*	Krejzová (1977)	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Reticulitermes lucifugus	*Entomophthora sp.*	Krejzová (1971)	L-Petri dish	Direct contact, various spp.	Medium mortality to various spp.	Inconclusive	Inconclusive	
Reticulitermes lucifugus	*Entomophthora destruens*	Krejzová (1972)	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Reticulitermes lucifugus	*Isaria fumosorosea*	Krejzová (1976)	L-Petri dish	Direct contact	Medium mortality	Inconclusive	Inconclusive	
Reticulitermes speratus	*Aspergillus niger*	Suzuki (1991, 1995)*	L-Petri dish	Direct contact/ Feeding	Medium mortality	Inconclusive	Inconclusive	
Reticulitermes speratus	*Beauveria bassiana*	Suzuki (1991, 1995)*	L-Petri dish	Direct contact/ Feeding	Medium mortality	Inconclusive	Inconclusive	
Reticulitermes speratus	*Beauveria bassiana*	Shimizu and Yamaji (2002)	L-Petri dish	Direct contact	High mortality, but reduced when termites are in larger groups	Inconclusive	Inconclusive	
Reticulitermes speratus	*Isaria fumosorosea*	Suzuki (1991, 1995)*	L-Petri dish	Direct contact/ Feeding	Medium mortality	Inconclusive	Inconclusive	
Reticulitermes speratus	*Isaria sp.*	Shimizu and Yamaji (2002)	L-Petri dish	Direct contact	High mortality, but reduced when termites are in larger groups	Inconclusive	Inconclusive	
Reticulitermes speratus	*Metarhizium anisopliae*	Suzuki (1991, 1995)*	L-Petri dish	Direct contact/ Feeding	High mortality	Positive	Inconclusive	P
Reticulitermes speratus	*Metarhizium anisopliae*	Shimizu and Yamaji (2002) also reported in Shimizu and Yamaji (2003)	L-Petri dish	Direct contact	High mortality, but reduced when termites are in larger groups	Inconclusive	Inconclusive	
Reticulitermes virginicus	*Aspergillus flavus*	Beal and Kais (1962)	L-Petri dish	Direct contact	80% mortality within 12 d	Inconclusive	Inconclusive	
Reticulitermes sp.	*Beauveria bassiana*	Kramm and West (1982)	L-Petri dish	Direct contact and gut activity	High mortality within 5d, fungus can grow after passage through the gut	Positive	Inconclusive	P
Reticulitermes sp.	*Gliocladium virens*	Kramm and West (1982)	L-Petri dish	Direct contact and gut activity	High mortality within 10d, fungus can grow after passage through the gut	Positive	Inconclusive	P
Reticulitermes sp.	*Metarhizium anisopliae*	Kramm and West (1982)	L-Petri dish	Direct contact and gut activity	High mortality within 1d, fungus can grow after passage through the gut	Positive	Inconclusive	P

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Reticulitermes sp.	*Metarhizium anisopliae*	Kramm et al. (1982)	L-Petri dish	Direct contact and transfer	High mortality, transferred to naïve termites	Positive	Inconclusive	P
Schedorhinotermes javanicus	*Metarhizium anisopliae*	Sukartana*, reported in Sukartana et al. (2000)*	L-Petri dish	Direct contact, unknown concentrations	High mortality	Positive	Inconclusive	P, C, N
Termitidae								
Unknown mound termite	*Beauveria bassiana*	Padmaja and Kaur (2001)*	L-Mound	Introduction in collected mound	High mortality	Positive	Inconclusive	N
Cornitermes cumulans	*Beauveria bassiana*	Fernandes and Alves (1991)	F-Mound	Direct introduction in the mound, as a mycoinsecticide	High mortality	Positive	Positive	
Cornitermes cumulans	*Beauveria bassiana*	Fernandes and Alves (1992)	L-Petri dish	Strain selection	Various mortality, strain 868 most virulent	Positive	Positive	
Cornitermes cumulans	*Beauveria bassiana*	Fernandes and Alves (1992)	F-Mound	Direct introduction in the mound, as a mycoinsecticide	High mortality	Positive	Positive	
Cornitermes cumulans	*Beauveria bassiana*	Alves et al. (1995)	F-Mound	Direct introduction in the mound, various size	Small nests are easily killed but a large amount of conidia is necessary to kill large nests	Positive	Positive	
Cornitermes cumulans	*Beauveria bassiana*	Neves and Alves (1999)	F-Mound	Direct introduction in the mound in association with Imidacloprid	High mortality, apparent synergy which allow the use of a small amount of chemical and fungi	Positive	Positive	
Cornitermes cumulans	*Beauveria bassiana*	Neves and Alves (2000a)	L-Petri dish	In association with Imidacloprid	Reduction of grooming activity and increased mortality	Positive	Positive	
Cornitermes cumulans	*Beauveria bassiana*	Neves and Alves (2000b)	L-Petri dish	Direct contact, strain selection	Highest mortality with strain 447	Positive	Positive	
Cornitermes cumulans	*Beauveria bassiana*	Neves and Alves (2004)	L-Petri dish	Direct contact, SEM preparation	Adhesion and penetration, death of the insects	Inconclusive	Inconclusive	
Cornitermes cumulans	*Beauveria bassiana*	Guirado et al. (2009)*	F-Mound	Directly in the mound as powder	No mortality	Negative	Negative	
Cornitermes cumulans	*Beauveria bassiana*	Toscano et al. (2010)*	F-Mound	Directly in the mound	Some mortality in small nests	Positive	Inconclusive	V
Cornitermes cumulans	*Metarhizium anisopliae*	Fernandes and Alves (1991)	L-Petri dish	Direct introduction in the mound, as a mycoinsecticide	High mortality	Positive	Positive	
Cornitermes cumulans	*Metarhizium anisopliae*	Fernandes and Alves (1992)	L-Petri dish	Strain selection	Various mortality, strains 865 and 866 most virulent	Positive	Positive	
Cornitermes cumulans	*Metarhizium anisopliae*	Fernandes and Alves (1992)	F-Mound	Direct introduction in the mound, as a mycoinsecticide	High mortality	Positive	Positive	
Cornitermes cumulans	*Metarhizium anisopliae*	Alves et al. (1995)	F-Mound	Direct introduction in the mound, various size	Small nests are easily killed but a large amount of conidia is necessary to kill large nests	Positive	Inconclusive	V
Cornitermes cumulans	*Metarhizium anisopliae*	Neves and Alves (1999)	F-Mound	Direct introduction in the mound in association with Imidacloprid	High mortality, apparent synergy which allow the use of a small amount of chemical and fungi	Positive	Positive	
Cornitermes cumulans	*Metarhizium anisopliae*	Neves and Alves (2000a)	L-Petri dish	In association with Imidacloprid	Reduction of grooming activity and increased mortality	Positive	Positive	
Cornitermes cumulans	*Metarhizium anisopliae*	Neves and Alves (2000b)	L-Petri dish	Direct contact, strain selection	Highest mortality with strain 1037	Positive	Positive	
Cornitermes cumulans	*Metarhizium anisopliae*	Neves and Alves (2004)	L-Petri dish	Direct contact, SEM preparation	Adhesion and penetration, death of the insects	Inconclusive	Inconclusive	
Cornitermes cumulans	*Metarhizium anisopliae*	Guirado et al. (2009)*	F-Mound	Directly in the mound with 1L of water	High mortality, only when mixed with water.	Positive	Inconclusive	V, N
Cornitermes cumulans	*Metarhizium anisopliae*	Toscano et al. (2010)*	F-Mound	Directly in the mound	Low mortality	Inconclusive	Inconclusive	
Macrotermes michaelseni	*Beauveria bassiana*	Gitonga (1996)*, also reported in Gitonga et al. (1995)*	L-Petri dish	Direct contact, strain selection	High mortality	Positive	Inconclusive	P
Macrotermes michaelseni	*Metarhizium anisopliae*	Gitonga, 1996*, also reported in Gitonga et al. (1995)*	L-Petri dish	Direct contact, strain selection	High mortality	Positive	Inconclusive	P
Macrotermes michaelseni	*Metarhizium anisopliae*	Gitonga (1996)*	F	Bait/Direct blown into the nest	Incomplete control	Inconclusive	Inconclusive	

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Macrotermes michaelseni	*Metarhizium anisopliae*	Mburu et al. (2009)	L-Petri dish	Direct contact/ olfaction	Most virulent strains were avoided	Negative	Negative	
Macrotermes michaelseni	*Beauveria bassiana*	Mburu et al. (2009)	L-Petri dish	Direct contact/ olfaction bioassay	Most virulent strains were avoided	Negative	Negative	
Macrotermes natalensis	*Beauveria bassiana*	Reported in Langewald et al. (2003)*	L-Petri dish	Unknown	High mortality	Inconclusive	Inconclusive	
Macrotermes natalensis	*Metarhizium anisopliae*	Reported in Langewald et al. (2003)*	L-Petri dish	Unknown	High mortality	Inconclusive	Inconclusive	
Macrotermes subhyalinus	*Beauveria bassiana*	Abebe (2002)*	L-Petri dish	Soil from mound, direct contact	High mortality	Positive	Inconclusive	P
Macrotermes subhyalinus	*Cordycepioideus sp.*	Ochiel et al. (1997) and Ochiel (1995)*	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Macrotermes subhyalinus	*Cordycepioideus sp.*	Ochiel et al. (1997) and Ochiel (1995)*	F-mound	Treated soil around mound	Relative high mortality	Inconclusive	Inconclusive	
Macrotermes subhyalinus	*Isaria fumosorosea*	Ochiel (1995)*	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Macrotermes subhyalinus	*Metarhizium anisopliae*	Abebe (2002)*	L-Petri dish	Soil from mound, direct contact	High mortality with strain ICIPE 30	Positive	Inconclusive	P
Macrotermes subhyalinus	*Metarhizium anisopliae*	Abebe (2002)*	F-Mound	Injection directly in the mound	Reduction of activity	Positive	Inconclusive	V
Macrotermes sp.	*Metarhizium anisopliae*	Maniania et al. (2002)*	F-Maize field	Granules application at planting	Reduced plant damage	Positive	Inconclusive	V
Microcerotermes beesoni	*Beauveria bassiana*	Singha et al. (2006)*	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Microcerotermes beesoni	*Metarhizium anisopliae*	Singha et al. (2006)*	L-Petri dish	Direct contact	High mortality	Inconclusive	Inconclusive	
Microcerotermes sp.	*Metarhizium anisopliae*	Krutmuang and Mekchay (2005)*, also reported in Krutmuang (1996)*	L-Petri dish	Direct contact / Feeding	High mortality	Positive	Inconclusive	P
Microcerotermes sp.	*Metarhizium anisopliae*	Gutiérrez et al. (2005)	L-Petri dish	Direct contact	High mortality at high dosage	Positive	Inconclusive	P, C
Microcerotermes sp.	*Paecilomyces lilacinus*	Gutiérrez et al. (2005)	L-Petri dish	Direct contact	High Mortality but also high control mortality	Positive	Inconclusive	P, N
Microtermes obesi	*Beauveria bassiana*	Singha et al. (2010)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P, N
Microtermes obesi	*Beauveria bassiana*	Singha et al. (2011)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Microtermes obesi	*Beauveria bassiana*	Singha et al. (2011)	F-Tree	Direct injection in tea bush	Reduced termite activity	Positive	Inconclusive	V, N
Microtermes obesi	*Metarhizium anisopliae*	Singha et al. (2010)*	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P, N
Microtermes obesi	*Metarhizium anisopliae*	Singha et al. (2011)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Microtermes obesi	*Metarhizium anisopliae*	Singha et al. (2011)	F-Tree	Direct injection in the infested tea bush	Reduced termite activity	Positive	Inconclusive	V, N
Microtermes sp.	*Metarhizium anisopliae*	Maniania et al. (2002)*	F-Maize field	Granules application at planting	Reduced plant damage	Positive	Inconclusive	V
Nasutitermes coxipoensis	*Metarhizium anisopliae*	Albuquerque et al. (2005)	L-Petri dish	Direct contact	High mortality in 3-7 d.	Positive	Inconclusive	P
Nasutitermes exitiosus	*Absidia coerulea*	Hänel (1982b)	L-Petri dish	Direct contact	No mortality	Negative	Negative	
Nasutitermes exitiosus	*Conidiobolus obscurus*	Hänel (1982b)	L-Petri dish	Direct contact	High mortality at high dosage	Inconclusive	Inconclusive	
Nasutitermes exitiosus	*Entomophthora virulenta*	Hänel (1982b)	L-Petri dish	Direct contact	High dosage required	Inconclusive	Inconclusive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Hänel (1981)	L-Petri dish	Direct contact	High mortality at high dosage	Positive	Positive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Hänel (1982b)	L-Petri dish	Direct contact	High mortality	Positive	Positive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Hänel (1982a)	L-Petri dish	Direct contact	High mortality	Positive	Positive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Hänel and Watson (1983)	F-Mound	Treatment at feeding site and nursery region	Colony control not consistent	Inconclusive	Inconclusive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Milner (1991)*	L- Petri dish	Direct contact	High mortality	Positive	Positive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Rath and Tidbury (1996)	L-Petri dish	Direct contact, high concentration	High mortality	Positive	Positive	

Termite species	Pathogen	References	Laboratory or field[a]	Protocol	Results	Authors interpretation	Re-interpretation	Reason[b]
Nasutitermes exitiosus	*Metarhizium anisopliae*	Milner et al. (1997a)	L-Petri dish	Direct contact, humidity selection	High mortality, 93% RH needed for sporulation	Positive	Positive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Milner et al. (1998a)	L-Petri dish	Direct contact, strain selection	High mortality	Positive	Positive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Staples and Milner (2000b)*	F-mound	Bait on the mound, direct inoculation in the nest	Various results depending on the protocol. Exposed termites have a difficulty to return to the nests due to repellency	Inconclusive	Inconclusive	
Nasutitermes exitiosus	*Metarhizium anisopliae*	Milner (2003)	F-mound	Directly blown in the nursery region	Death of colonies treated with high quantity of conidia	Inconclusive	Inconclusive	
Nasutitermes voeltzkowi	*Metarhizium anisopliae*	Chouvenc et al. (2009)	L-Petri dish	Direct contact	Moderate mortality at high dosage	Negative	Negative	
Nasutitermes sp.	*Beauveria bassiana*	Malagodi and Veiga (1994)	L-Petri dish	Direct contact	High mortality at high dosage	Positive	Inconclusive	P
Nasutitermes sp.	*Metarhizium anisopliae*	Malagodi and Veiga (1994)	L-Petri dish	Direct contact	High mortality at high dosage	Positive	Inconclusive	P
Nasutitermes sp.	*Metarhizium anisopliae*	Gutiérrez and Saldarriaga (2004)	L-Petri dish	Direct contact	high mortality	Inconclusive	Inconclusive	
Odontotermes brunneus	*Beauveria bassiana*	Khader Khan et al. (1991)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes brunneus	*Beauveria bassiana*	Khader Khan et al. (1993a)	L-Petri dish	Direct contact, effect of temperature	High mortality at 25°C	Positive	Inconclusive	P
Odontotermes brunneus	*Isaria fumosorosea*	Khader Khan et al. (1991)	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Odontotermes brunneus	*Metarhizium anisopliae*	Khader Khan et al. (1991)	L-Petri dish	Direct contact	Medium mortality	Positive	Inconclusive	P
Odontotermes brunneus	*Metarhizium anisopliae*	Khader Khan et al. (1993a)	L-Petri dish	Direct contact, effect of temperature	High mortality at 25°C	Positive	Inconclusive	P
Odontotermes brunneus	*Metarhizium flavoridae*	Khader Khan et al. (1991)	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Odontotermes brunneus	*Paecilomyces lilacinus*	Khader Khan et al. (1991)	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Odontotermes formosanus	*Metarhizium anisopliae*	Dong et al. (2007), also reported in Dong et al. (2009)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes guptai	*Metarhizium anisopliae*	Swaran and Varma (2004)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes latericus	*Beauveria bassiana*	Reported in Langewald et al. (2003)*	L-Petri dish	Unknown	High mortality	Inconclusive	Inconclusive	
Odontotermes latericus	*Metarhizium anisopliae*	Reported in Langewald et al. (2003)*	L-Petri dish	Unknown	High mortality	Inconclusive	Inconclusive	
Odontotermes obesus	*Aspergillus flavus*	Sannasi (1968)	L-Petri dish	Direct contact, on dealate	High mortality	Positive	Inconclusive	P, N
Odontotermes obesus	*Beauveria bassiana*	Khader Khan et al. (1993b)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes obesus	*Beauveria bassiana*	Gurusubramanian et al. (1999)	L-Container	Inoculated soil	High mortality at high dosage	Positive	Inconclusive	P, C
Odontotermes obesus	*Beauveria bassiana*	Kakde et al. (2005)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes obesus	*Beauveria bassiana*	Tamuli and Gurusubramanian (2011)*	L-Jar	Inoculated soil	High mortality	Positive	Inconclusive	P
Odontotermes obesus	*Bipolaris tetramera*	Singh et al. (1976)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes obesus	*Isaria fumosorosea*	Khader Khan et al. (1993b)	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Odontotermes obesus	*Metarhizium anisopliae*	Khader Khan et al. (1993b)	L-Petri dish	Direct contact	Medium mortality	Positive	Inconclusive	P, C
Odontotermes obesus	*Metarhizium anisopliae*	Kakde et al. (2005)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes obesus	*Metarhizium flavoridae*	Khader Khan et al. (1993b)	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Odontotermes obesus	*Paecilomyces lilacinus*	Khader Khan et al. (1993b)	L-Petri dish	Direct contact	Low mortality	Negative	Negative	
Odontotermes sp.	*Metarhizium anisopliae*	Balachander et al. (2009)	L-Petri dish	Direct contact	High mortality	Positive	Inconclusive	P
Odontotermes sp.	*Metarhizium anisopliae*	Remadevi et al. (2010)	L-Petri dish	Direct contact, strain selection	High mortality	Positive	Inconclusive	P, C

[a]L= Lab, F= Field
[b]Explanation for disagreeing with the authors' interpretation. P=The experiment was performed in a Petri dish or equivalent, with poor biological relevancy to the given termite species and remains a screening test. C=Mortality was observed only with high concentrations of the pathogen which cannot be applied in the field. N=No data were provided to support the claim. V=The variability in the results shows that control was not consistent.
*Non-peer reviewed journal

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