

**Ecology of termites from the genus *Nasutitermes* (Termitidae: Nasutitermitinae) and potential for science-based development of sustainable pest management programs**

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1 **Ecology of termites from the genus *Nasutitermes* (Termitidae: Nasutitermitinae) and**  
2 **potential for science-based development of sustainable pest management programs**

3

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29 **Key Message**

- 30 • We reviewed the taxonomic status of *Nasutitermes*, which is currently the most  
31 diverse termite genus, has a particularly complex taxonomic history, and includes  
32 some major pest species.
- 33 • We performed a comparative literature analysis, especially concerning the type-  
34 species *N. corniger*, while filtering available information concerning its biology  
35 through the prism of termite control.
- 36 • We critically examined the existing management of *N. corniger* (synthetic chemical  
37 products, botanical insecticides towards various targets, and biological control) to lead  
38 to the development of innovative management tools and strategies.

39

40 **Author Contribution Statement**

41 IB conceived the first draft. RC wrote the taxonomic history part and corrected biological  
42 part. EH, AR and NA corrected and greatly contributed to the pest management part. MF  
43 made all the drawings of *N. corniger*'s colony. All authors read, corrected and approved the  
44 manuscript.

45

46 **Abstract**

47           The genus *Nasutitermes* is among the most abundant wood-feeding Termitidae and an  
48 extremely diverse and heterogeneous group in terms of its biogeography and morphology.  
49 Despite the major role of several *Nasutitermes* species as structural pests, the phylogenetic  
50 status of this genus is still unclear, alongside with a confused taxonomy and species  
51 identification remaining difficult. The first aim of this review was thus to gather and discuss  
52 studies concerning the taxonomic status of the genus *Nasutitermes*, in order to clarify this  
53 crucial point. Then, our goal was to gain new insights into the management of *N. corniger*,  
54 considered to be the most economically detrimental pest of this genus in South America and a  
55 *Nasutitermes* model species, while filtering available information concerning its biology  
56 through the prism of termite control, as well as critically examine the existing methods. We  
57 indeed strongly believe that increasing our knowledge of this species' biological strategies is  
58 the key to progress in the challenging question of their sustainable management.

59

60

61

62 **Keywords:** Taxonomic history, *Nasutitermes corniger*, Termitidae, sustainable management,  
63 IPM, antimicrobial and insecticidal botanical extracts.

64

## 65 **1. Introduction**

66 The species causing the most considerable damage to tropical agriculture belong to  
67 four of the eight subfamilies of higher termites (Termitidae), and Nasutitermitinae is one of  
68 them (Rouland-Lefèvre 2011; Krishna et al. 2013). The genus *Nasutitermes* is among the  
69 most abundant wood-feeding Nasutitermitinae in the tropics and several *Nasutitermes* species  
70 are important structural pests (Constantino 2002; Fontes and Milano 2002). This genus  
71 comprises a diverse and heterogeneous group of species (Miura et al, 2000). The distributional  
72 patterns of *Nasutitermes* species were probably shaped by environmental conditions and  
73 historical factors, such as continental drift, orogeny, and Quaternary climatic variations  
74 (Miura et al, 2000).

75 As currently defined, *Nasutitermes* does not comprise a monophyletic group of species  
76 (Eggleton 2001; Inward et al. 2007; Roy et al. 2014), its taxonomy is confused, and accurate  
77 species identification is very difficult. Many nasute species that do not belong to the  
78 *Nasutitermes* clade remain nested within *Nasutitermes*, generating taxonomic confusion,  
79 while misidentifications and nomenclatural errors are frequent (Gush et al. 1985; Traniello et  
80 al. 1985; Constantino 2000; 2002; Scheffrahn et al. 2002; Scheffrahn et al. 2005a; Scheffrahn  
81 et al. 2005b). A comprehensive taxonomic revision of the genus is highly necessary, but has  
82 never been attempted due to the enormous difficulties involved.

83 However, despite this heterogeneity, some aspects, such as nest building (Thorne et al.  
84 1996; Fuller and Postava-Davignon 2014), soldiers' defense strategies (Prestwich 1979) and  
85 hindgut microbiome role in symbiosis (Brune 2014), are well known for several *Nasutitermes*  
86 species. Yet, this information could be more clearly highlighted and discussed in the  
87 perspective of pest management to exploit at its most and face the growing importance of  
88 *Nasutitermes* pest species. These termites live in a large range of habitats in urban,  
89 anthropized, disturbed and natural environments, in dry as well as in moist conditions and at

90 elevations of up to 1000 m (Scheffrahn et al. 2005a; Bustamante and Martius 1998; Dunn and  
91 Messier 1999, Vasconcellos and Moura 2010, Mello et al. 2014, Lima et al. 2013). This  
92 versatility, alongside with changes in urban soil occupation in the last few decades, leads to  
93 an increasing infestation in large buildings which are full of structural voids, narrow fissures  
94 and wood (Fontes and Milano 2002).

95 In this paper, we thus gathered and commented studies on taxonomic history and  
96 current status of genus *Nasutitermes*, in order to clarify this crucial point. Indeed, taxonomy  
97 provides an essential framework, as no effective and sustainable management can be set up  
98 without precisely identifying and describing the intended species.

99 We also aimed to gain new insights into the biology of *N. corniger* as a *Nasutitermes*  
100 model species, in the perspective of improving termite control. Better insights into these  
101 aspects would indeed contribute to the development of more adapted and efficient control  
102 methods, as highlighted by Scharf (2015) in a recent review.

103 Eventually, we critically examined the existing management methods against *N.*  
104 *corniger* and lastly underlined the fact that termites are also beneficial, playing a key role in  
105 the wood decomposition process.

106

## 107 **2. Taxonomic history of genus *Nasutitermes* Dudley, 1890**

108 *Nasutitermes* has a complex taxonomic history and many of the species currently  
109 included in this genus have been classified in other termite genera, while several species  
110 previously included in *Nasutitermes* have been transferred to other genera.

111 Our current taxonomic system begins with Linnaeus (1758), who described a single  
112 termite genus, *Termes*, which means termite in Latin. All termite species were classified in  
113 genus *Termes* for nearly a century after Linnaeus. In 1781 the British naturalist Henry  
114 Smeathman, described *Nasutitermes arborum* (as *Termes arborum*) from Sierra Leone,

115 Africa, which was the first species of *Nasutitermes* to be formally named. Smeathman (1781)  
116 also presented information on its biology, nests, and damage to houses.

117 Termite classification started to change in the second half of the 19<sup>th</sup> century, when the  
118 German entomologist H.A. Hagen was the main authority on termite taxonomy. Hagen's  
119 (1858) monograph on world termites listed seven species of *Nasutitermes*, all of them  
120 included in the subgenus *Termes* (*Eutermes*) Heer, 1849. *Eutermes* was defined based on  
121 wing venation and in Hagen scheme it included a heterogeneous group of species, currently  
122 classified in several distinct genera.

123 The concept of “*Eutermes*” was restricted by Brauer (1868) to include only the termite  
124 species with a nasute soldier. Müller (1873), Froggatt (1897), and Silvestri (1903) adopted  
125 Brauer's definition and also raised *Eutermes* to the status of a genus. During that period,  
126 “*Eutermes*” was equivalent to our current definition of the subfamily Nasutitermitinae, and  
127 included all known species of *Nasutitermes*.

128 After the discovery of many new termite species with nasute soldiers, Holmgren  
129 (1910, 1912) subdivided the genus *Eutermes* into several subgenera. In Holmgren's system,  
130 subgenus *Eutermes* (*Eutermes*) was approximately equivalent to our current definition of  
131 genus *Nasutitermes*.

132 The name *Nasutitermes* itself appears for the first time in a paper about termites of  
133 Panama (Dudley 1890). Because Dudley did not provide a formal taxonomic description and  
134 did not include any species in the new genus, several authors overlooked the new name. It is  
135 important to note that formal international rules of nomenclature did not exist in 1890 (the  
136 first edition of the Code was published in 1905). Despite its limitations, Dudley's description  
137 satisfies the rules of nomenclature established in the first edition of the Code, and is therefore  
138 an available name.

139 Banks (1918) revealed a major problem with the previous use of the name  
140 “*Eutermes*”: its type-species, *Eutermes debilis*, a fossil, was identified as a species of  
141 *Microcerotermes*, a genus with mandibulate soldiers not related to the nasutes. In the same  
142 paper, Banks adopted the name *Nasutitermes* Dudley, 1890 for the termites with nasute  
143 soldiers. The status of the name *Eutermes* is still considered uncertain and it has not been used  
144 for living termites. However, many species currently placed in *Nasutitermes* appeared in the  
145 literature under the name “*Eutermes*” for a couple of decades, including the important  
146 monographs published by Holmgren (1909, 1910, 1912).

147 The name *Nasutitermes* was widely adopted after 1918. Initially, it included all  
148 species with nasute soldiers (= subfamily Nasutitermitinae), and was later subdivided into  
149 several new subgenera and genera. Snyder's (1949) world catalog of termites lists about 400  
150 species of nasute termites, classified into 25 different genera; among them, 190 species were  
151 listed under the genus *Nasutitermes*.

152 Today, *Nasutitermes* is the most diverse termite genus, with 254 valid species  
153 (Krishna et al. 2013, updated). It is present in all biogeographical regions, distributed as  
154 follows: Oriental 114, Neotropical 78, Papuan 20, Ethiopian 19, Australian 19, Palearctic 14,  
155 and Nearctic 01. As shown in Figure 1, new species of *Nasutitermes* have been discovered  
156 continually since the end of the 19<sup>th</sup> century. Variation in the description rate is related to the  
157 number of active termite taxonomists, which was larger during the first half of the 20<sup>th</sup>  
158 century. The total number of species is likely to increase in the future.

159 The species currently included in genus *Nasutitermes* do not form a monophyletic  
160 group (Inward et al. 2007). Some are quite distinct from the type species (*N. corniger*) and  
161 were included in *Nasutitermes* when this genus comprised most Nasutitermitinae. The  
162 reexamination of the status of these species has resulted in changes in the classification, with  
163 the description of new genera and reassignment of some species to other known genera of



164 Nasutitermitinae. For instance, several species previously included in *Nasutitermes* were  
165 transferred to *Cortaritermes* by Mathews (1977), Fontes (1998), and Cuzzo et al. (2015).  
166 The name *Nasutitermes*, however, will always be associated with its type-species, *N.*  
167 *corniger*.

168

### 169 **3. *Nasutitermes corniger* (Motschulsky, 1855) as a model species**

170 *Nasutitermes corniger* is a neotropical species which occurs natively from southern  
171 Mexico to northern Argentina and in the Caribbean islands, and it is an invasive species in  
172 the Bahamas, Florida and New Guinea (Figure 2) (Scheffrahn et al. 2005a; Evans et al. 2013).  
173 In the latter area, it may have been introduced accidentally due to human transport  
174 (Scheffrahn et al. 2005b). It is widely distributed in the neotropics, with high adaptability to a  
175 wide range of habitats (Scheffrahn et al. 2002). *Nasutitermes corniger* is the most important  
176 pest species of this genus in the New World (Constantino 2002; Fontes and Milano 2002) and  
177 its biology is relatively well-known.

178

#### 179 **3.1 Biology, ecology, and behavior of *Nasutitermes corniger***

180

##### 181 **Apterous line: tasks and morphological polyethism**

182 *Nasutitermes corniger* is a social insect that has colonies that can contain up to  
183 900,000 individuals (Dunn and Messier 1999; Thorne 1984). A colony is composed of  
184 workers, soldiers, and imagoes. In Termitidae, this structure originates from a common first  
185 stage of development, from which an apterous and an imaginal concurrently emerge. The  
186 imaginal line leads to the reproductive caste. From the apterous line the worker caste appears,  
187 followed by soldiers (Figure 3) (Lima et al. 2013).

188 Workers are primarily responsible for foraging, constructing and repairing the nest;  
189 carrying eggs and nursing; and feeding and grooming immature stages, soldiers, and  
190 reproductives as well as participating in defensive activities with soldiers (Thorne 1984).  
191 Soldiers are a defensive caste responsible for guarding the colony (Traniello 1981; Gazal et  
192 al. 2012; Verma et al. 2009). They also organize foraging by exploring new wood sources  
193 (Traniello 1981) and by regulating foraging activity. During nest defense, soldiers squirt from  
194 their nasus a sticky, odoriferous, irritating secretion to distances of more than three times their  
195 body length (Traniello 1981; McMahan 1982). All sterile forms (workers and soldiers) are  
196 blind and lucifugous (Thorne 1983; Scheffrahn et al. 2005a; Verma et al. 2009). These termite  
197 castes are 4 to 6 mm long, pale and soft bodied (Figure 4); mature in one year; and can live up  
198 to 5 years (Verma et al. 2009). As is typical for the genus *Nasutitermes*, workers show sexual  
199 dimorphism, with females conspicuously larger than males (Lima et al. 2013; Scheffrahn et  
200 al. 2005a; Jones 1980). Soldiers represent between 5 and 20% of a colony (Dunn and Messier  
201 1999; Thorne 1984). They are characterized by reduced mandibles and a modified cephalic  
202 projection (the nasus), giving its name to the genus (Thorne 1984). Both soldiers and workers  
203 are completely sterile, with vestigial reproductive organs.

204 In a recent study, Lima et al. (2013) studied caste polymorphism of *N. corniger*  
205 apterous line using morphometric and discriminant analysis. Based on the comparison of the  
206 length of the antenna, thorax and metatibia, they highlighted two morphological types in  
207 presoldiers and soldiers, and two lines of development for workers. These elements  
208 demonstrate that morphological studies of *N. corniger* still remain crucial to increase the  
209 knowledge of the caste system in this species. Coupled with analytical and statistical tools,  
210 they can still lead to new discoveries. In addition to the rigorous determination of  
211 morphological types, these elements contribute to improving the understanding of  
212 individuals' interactions inside the colony. Lima et al. (2013) emphasized the fact that

213 knowing whether the different morphological types perform different tasks would help in  
214 understanding the behavioral dynamics in termites' societies. Former studies have, for  
215 example, shown that the behavior of each caste is significantly different during nest repair and  
216 nest expansion (McMahan 1970). Moreover, molecular approaches also offer promise for  
217 deciphering cryptic aspects of caste biology, potentially leading to insights for new control  
218 technologies (Scharf et al., 2015).

219

### 220 **Nymphal line: Description of the reproductive strategies**

221 Imagoes are of three types: primary reproductives (queens and kings), alates, and  
222 adultoids (Thorne 1984). They have fully developed eyes and are winged and pigmented  
223 (Scheffrahn et al. 2005a; Verma et al. 2009; Thorne 1983). The primary reproductives are the  
224 imagoes that initiated the colony after the dispersal flight. Alates are produced seasonally and  
225 leave the nest after spending 5 to 8 months within the parental colony, while adultoids are  
226 replacement reproductives derived from alates that did not disperse (Thorne 1983).

227 Ergatoids are worker-like neotenic reproductives derived from immatures of the neuter  
228 line. They have two additional molts compared to worker's development. They are wingless,  
229 blind and are at the bottom of the fecundity hierarchy (Figure 3) (Thorne 1984).

230 Mature colonies of *N. corniger* release large numbers of alates during massive  
231 crepuscular nuptial flights (35% of the colony biomass and 5000 to 25000 individuals on  
232 average), usually after rain (Thorne 1983). Royal couples are formed, find moist places with  
233 wood food, shed their wings, and remain together throughout the life cycle of the colony.  
234 Queens have a physogastric abdomen (due to ovariole growth), are capable of laying  
235 approximately 3000 eggs per day, and can live up to 25 years (Scheffrahn et al. 2005a). The  
236 eggs are yellow to white and incubate for 50 to 60 days before hatching (Verma et al. 2009).

237 Colonies of *N. corniger* have the largest number of primary queens per colony and the  
238 highest proportion of polygynous colonies, as 20 to 25% of mature colonies are headed by  
239 multiple unrelated primary reproductives (Thorne 1984; Atkinson and Adams 1997; Hartke  
240 and Rosengaus 2013). The tolerance of several queens in polygynous nests was hypothesized  
241 to be due to the high individual cost of intensively laying at high rates, and this phenomenon  
242 is apparently inversely related to the mean weight of queens (Adams and Atkinson 2008).  
243 However, a study performed by Hartke and Rosengaus regarding the cost of pleometrosis  
244 compared with colony foundation by monogamous pairs demonstrated that this strategy is  
245 disadvantageous for the colony's fitness (Hartke and Rosengaus 2013). Thus, mature  
246 polygamous nests of *N. corniger* may not be established via pleometrosis, but may imply  
247 other phenomena, such as the coalescence of young monogamous colonies. In fact, polygyny  
248 in *N. corniger*, as in the case of other Isoptera and some Hymenoptera, is not accompanied by  
249 nepotism because no data showed that workers care for their mothers more than the other  
250 queens (Atkinson et al. 2008). Likewise, experimental young colonies easily merged under  
251 laboratory conditions (Hartke and Rosengaus 2013). These results highlight the fact that  
252 further studies may be useful to understand the exact process as well as the ecological  
253 advantages of this phenomenon of colony fusion. Alongside its feeding habits and the aspects  
254 related to nesting, these reproduction mechanisms may play a part in the species' success in  
255 colonizing space, thus making *N. corniger* a major urban pest (Mello et al. 2014).

256

### 257 **Role of the nest: from structural protection to immunity enhancement**

258 Nests of *N. corniger* (Figure 5) are constructed on trees, bases of trunks, in secluded  
259 places of buildings or, less often, on the open soil (Scheffrahn et al. 2005a). These nests are  
260 single or polycalic, from ovoid to conical in form, with dimensions ranging up to 90 cm in  
261 height and 40 cm in width (Dunn and Messier 1999; McMahan 1982; Levings and Adams

262 1984; Scheffrahn et al. 1990). The nests have three parts: a superficial area with a thin skin of  
263 carton, which can exclude predators and prevent desiccation and flooding conditions  
264 (McMahan 1982; Fuller and Postava-Davignon, 2014); a middle part consisting of  
265 interconnecting galleries and chambers made of hard and dense carton (McMahan 1982); and  
266 a queen chamber located near the center of the nest (Thorne 1980). Additionally, carton-  
267 covered tunnels radiate from the nest and provide protection to termites during foraging  
268 (Levings and Adams 1984). This particular organization represents a challenge in termite  
269 management, because nests are often distant from infestation sites and are so structurally  
270 sound, *Nasutitermes* control can thus often be difficult (Fontes and Milano 2002; Gazal et al.  
271 2012).

272         The stercoral carton used by termite workers during foraging, constructing or repairing  
273 processes is a black substance mainly composed of masticated wood and feces, cemented with  
274 salivary secretions (Postava-Davignon 2010; Traniello 1981; McMahan 1982). In addition,  
275 some other chemical or biological substances can also be incorporated inside this material.  
276 For example,  $\beta(1,3)$ -glucanase activity was recently discovered in the *N. corniger* nest carton  
277 due to the presence of the native tGNBP-2 protein. By cleaving and releasing pathogenic  
278 components, it participates in the colony's immunological defense system against infections  
279 (Bulmer et al. 2004; 2009). Also, preliminary results obtained on *N. acajutlae* highlighted  
280 that, in general, fewer bacteria and fungi were observed inside the nests compared to the soil  
281 and trails (Postava-Davignon 2010). Thus, *Nasutitermes* nests are effective structures that  
282 allow the insects to survive in their environment, and antimicrobial defense integrated in the  
283 structure can help termites to enhance their immunity. This perfectly exemplifies the richness  
284 of defense strategies among insect colonies. Based on this information, Bulmer et al. (2009)  
285 developed a glycomimetic molecule blocking tGNBP-2 using rational design, which increases  
286 infection and death rate of exposed termites and can be used as an alternative control method.

287 This work clearly demonstrated that understanding termite biology is key to their sustainable  
288 management, as well as the resolution of product engineering and development issues.

289

290 **Pheromone biology: communication, recruitment, modulation**

291 Chemical odor trails are produced by the sternal gland (Stuart 1963). This gland is  
292 located on the fifth abdominal sternite and is composed of modified epidermal cells (Traniello  
293 and Busher 1985). Soldiers' sternal glands are smaller, on average, than workers'. These  
294 sternal pheromones are implicated in several aspects of the colony life. When nest defense is  
295 necessary, soldiers release a secretion from their nasus, which contains a mixture of  
296 terpenoids and elicits alarm and defensive recruitment (Thorne 1984; Roisin et al. 1990).  
297 Pheromones also communicate information about the presence and location of food, are used  
298 to recruit more soldiers and workers, and can modulate caste differentiation, either positively  
299 or negatively (Traniello and Busher 1985; Scharf 2015).

300 Recruitment was formerly proposed to depend on the quantitative production of the  
301 pheromone (Traniello and Busher 1985). In fact, it was effectively measured that the  
302 worker/soldier concentration ratio was 0.2 times for compounds concentrated in *N. corniger*  
303 (Arab et al. 2006). Moreover, behavioral evidence for species, colony, and caste specificity of  
304 the trail pheromone were also presented (Dunn and Messier 1999; Arab et al. 2006). In  
305 particular, Arab et al. (2006) described that both *N. corniger* workers and soldiers preferred  
306 the trails made by conspecific soldiers over those from workers. Extracts from the same  
307 species, and more particularly from the same colony, were also demonstrated to be preferred  
308 (Arab et al. 2006). Dunn and Messier (1999) highlighted that soldiers are able to discriminate  
309 their own colony members from conspecific neighbors and strangers; therefore, they behave  
310 more aggressively toward neighbors, with which they are competing for resources and  
311 territory, compared to strangers.

312           If quantitative differences between soldiers' and workers' trail pheromones can help to  
313 regulate the foraging behavior of these termites, the chemical composition of the sternal gland  
314 secretions should also be taken into account. For example, chemical analysis identified  
315 neocembrene, dodecatrienol and trinervitatriene in the pheromone trail, with a ratio of  
316 dodecatrienol/neocembrene of 1:25 and a ratio of trinervitatriene/neocembrene of 1:2 in the  
317 sternal glands of *N. corniger*'s workers (Sillam-Dussès et al. 2010). Monocyclic 14-membered  
318 ring diterpene cembrene-A is also a common constituent of this trail and is a short-term alarm  
319 capable of orienting soldiers to an area of disturbance (Hall and Traniello 1985). Moreover,  
320 some other parameters may play an important role in trail following. For example, a study  
321 performed by Gazal et al. highlighted the significant effect of feces on the trail (Gazal et al.  
322 2014). Chemical analyses on the feces' composition, and behavioral studies implicating the  
323 identified compounds, may lead to valuable information that could help to improve the  
324 understanding of trail following mechanisms. This could be of importance to develop  
325 attractant or repulsive products in the context of an integrated pest management procedure. In  
326 addition to their crucial role for recruitment, chemical trails also probably exhibit  
327 antimicrobial activities and might be involved in the control of nest microbial competitors  
328 (Rosengaus et al. 2000). According to these results, studying the influence of the  
329 morphological type on potential specificity induction in trail preference could also lead to  
330 interesting results, besides contributing to the understanding of the social function of each  
331 morphological type inside a colony. Eventually, as primer pheromones from soldiers and  
332 other castes may also regulate caste homeostasis (Scharf et al., 2015), studying these  
333 compounds and their associated biology could potentially lead to insights for new control  
334 technologies.

335

336 **Food selection: a complex process**

337 *Nasutitermes corniger* feeds on dry, wet, or partially decomposed wood (He et al.  
338 2013). It has the ability to consume a large variety of wood, such as dead twigs and branches  
339 in trees, tree stumps, wood debris on the ground and structural wood, including framing,  
340 plywood, pressboard, hardwood handles, wooden artwork, fences and paper and derivatives in  
341 laboratory conditions (Scheffrahn et al. 2005a). However, the exact stimuli implicated in the  
342 finding and selection of food by *N. corniger* is still under evaluation.

343 *Nasutitermes corniger* was first described as having no significant consumption  
344 preference among different wood species, but with a strong preference for decayed over fresh  
345 wood (Bustamante and Martius 1998). However, further contradictory studies demonstrated a  
346 significant species preference under laboratory conditions (Gazal et al. 2010). Yet, consistent  
347 with the results obtained by Bustamante and Martius (1998), the choice was not shown to  
348 exclusively depend on the density. Concerning the stage of decay of the wood, a more recent  
349 study conducted by Gazal et al. (2012) confirmed the results of Bustamante and Martius.  
350 Whatever the tested species, decayed wood always recruited more individuals than undecayed  
351 wood in standard foraging arenas. The next step was to investigate whether the choice of the  
352 source of wood was attributed to physical or chemical factors. This work thus demonstrated  
353 the crucial role of the secondary metabolites produced during wood degradation in the choice  
354 of a food substrate by comparing impregnation of a neutral (filter paper) and of wood (fresh  
355 or decayed) substrate with weathered or unweathered *Eucalyptus grandis* wood extracts  
356 (Gazal et al. 2014).

357 Following these results, further studies should be performed on the identification and  
358 origin of the compounds linked to wood degradation and to investigate their action on wood's  
359 physicochemical properties. It may also be interesting to investigate the effect of weathered  
360 and unweathered extracts on a neutral wood substrate from which secondary metabolites  
361 would have been removed or on non-durable wood, such as *Pinus* sp. According to some



362 authors, the preference for decayed wood could be due to several factors. Decomposition may  
363 lead to an increase of nutrient availability and a facilitation of mastication during the process  
364 and the depolymerization of cellulose, making wood fibers easier to remove and compounds  
365 more degradable. Moreover, it is possible that wood degradation releases allelochemicals that  
366 influence the foraging behavior or trigger trail following. Decomposition is also associated  
367 with the presence of microorganisms, notably fungi, which are potential additional sources of  
368 nitrogen and vitamins for the termites (Vasconcellos and Moura 2010; Gazal et al. 2012;  
369 Gazal et al. 2014). In addition to improve the ecological and biological knowledge of the  
370 species, understanding the mechanisms of termites' food selection would play a central role in  
371 developing new techniques to control *N. corniger* in case of infestation, such as substrates for  
372 insecticide-impregnated baits, or prevent *N. corniger* colonization of buildings by orienting  
373 technological choices.

374

### 375 **Symbiosis and mutualism**

376 The insect gut is divided into three regions: the stomodeum (foregut), the mesenteron  
377 (midgut), and the proctodeum (hindgut). The foregut includes the crop, a food-storage organ.  
378 In termites, the hindgut is enlarged and subdivided into five segments (P1-P5). The crop is  
379 slightly acidic, whereas the hindgut is moderately alkaline, with anaerobic conditions (Bignell  
380 and Anderson 1980). In the third hindgut segment (P3 or paunch), a bacterial community has  
381 developed that confers certain important benefits to the termite. In fact, in the case of *N.*  
382 *corniger*, such as other higher termites (Termitidae), digestive enzymes are encoded both by  
383 the termite genome itself and by these symbiotic bacteria, as these species do not possess  
384 hindgut flagellate protozoa, contrary to lower termites for which these organisms are the  
385 sources of cellulases and hemicellulases (Warnecke et al. 2007). However, this microbiome  
386 appears to play a far more complex role than only being related to cellulose degradation, as in

387 nitrogen fixation (Prestwich and Bentley 1981; Tayasu et al. 1994). In the case of an arboreal  
388 species close to *N. corniger*, a metagenomic analysis of the hindgut-associated microbial  
389 community highlighted the presence of bacterial genes for cellulose and xylan hydrolysis and  
390 also provided information about the possible functional role of this community concerning  
391 free H<sub>2</sub> generation and CO<sub>2</sub>-reductive acetogenesis, alongside the identification of genes  
392 associated with nitrogen fixation (Warnecke et al. 2007). Metaproteome analysis of this  
393 community revealed the presence of proteins of known enzymatic functions in the case of *N.*  
394 *corniger*, thus permitting the reconstruction of the enzymatic pathways concerning transport,  
395 glucan binding, sugar fermentation, hydrogen metabolism, amino acid synthesis, and nitrogen  
396 fixation and assimilation (Burnum et al. 2010). These findings are complementary to the  
397 results previously obtained by Warnecke et al. (2007), although from all the isolated known  
398 proteins no enzyme involved in cellulose degradation could be observed. This may be due to  
399 methodic limitations, or because the cellulose native degradation may occur elsewhere than  
400 inside the termite hindgut.

401 Spirochetes, mostly from the *Treponema* genus, and Fibrobacteres, alongside an  
402 undetermined phylum (TG3), were the most abundant phyla of these *N. corniger* microbial  
403 symbionts and were established to be fiber-associated bacterial communities that significantly  
404 contribute to the cellulotic activity (He et al. 2013; Warnecke et al. 2007; Mikaelyan et al.  
405 2014). Warnecke et al. (2007) also demonstrated that gene modules coding for iron-only  
406 hydrogenase were bound to the genus *Treponema*, as well as marker genes linked to the  
407 acetogenesis pathway, and this process apparently dominates in *Nasutitermes* by  
408 Spirochaetes. In the actinobacterial community, well known for its role in organic matter  
409 decomposition, such as cellulose, five families (*Propionibacteriaceae*, *Streptomycetaceae*,  
410 *Cellulomonadaceae*, *Corynebacteriaceae* and *Rubrobacteraceae*) were identified for *N.*  
411 *corniger*, regardless of the geographical origin or feeding behavior (Lefebvre et al. 2009).

412           Regarding the apparent role of microbial symbionts concerning cellulose digestion and  
413 other essential metabolic functions, disrupting this effective equilibrium would be important  
414 in the continuous search for insecticidal products. In fact, it was demonstrated that modifying  
415 the carbon source allocated to the higher termite *N. takasagoensis* led to marked changes in the  
416 bacterial community structure, thus highlighting the delicateness of this relationship (Miyata  
417 et al. 2007). Moreover, in the case of an integrated pest management strategy, searching for  
418 products that exhibit antimicrobial activity seems to be a promising perspective (Shelton and  
419 Grace 2003).

420           Concurrent to this crucial symbiosis, other types of associations can be observed in  
421 termites' societies. In particular, ants could be associated with facultative or opportunistic  
422 mutualism where these insects use part of the termite nest, prey on live or dead workers,  
423 provide the termites with nitrogen nutrients and assist in nest protection. The frequency of *N.*  
424 *corniger* association with ant species depends, in particular, on the cost-benefit balance linked  
425 to predation risk. A Brazilian study demonstrated that Formicidae species richness in  
426 *Nasutitermes*' nests (*N. corniger* and *N. ephratae*) was significantly higher in abandoned  
427 nests, in 48 species, compared to active or decadent nests, in 6 and 8 species (Santos et al.  
428 2010). In the latter case, *Crematogaster acuta* (Fabricius) and *Ectatomma tuberculatum*  
429 (Olivier) were the most frequent species observed. *Monacis bispinosa* (Olivier), which is  
430 highly susceptible to the soldier frontal gland mixture and which do not prey on live termites,  
431 was the most frequently found species in common ants / *N. corniger* nests in Venezuela (Jaffe  
432 et al. 1995). *Crematogaster brevispinosa* (Mayr), an arboreal ant, has been observed in  
433 association with *N. corniger* in Brazil, sharing the same nest even if a physical barrier is built  
434 between the two communities. The participation of ants in nest protection and nutritional  
435 substrate supply thus appears to be another factor contributing to the success of *N. corniger*  
436 colonization.

437

### 438 **3.2 Pest management**

439 Synthetic chemical products, as active substances inhibiting wood degradation by termites  
440 and microorganisms, can be applied through soil, wood treatment, or chemical fumigations,  
441 before or after infestation (Paiva et al. 2011) (Table 1). Excellent reviews or technical reports,  
442 such as those by Schultz et al. (2007; 2008) concerning wood preservation, Verma et al.  
443 (2009) on the biological control of termites, or the expert group on termite biology and  
444 management of the United Nations Environment Program (UNEP 2000), have taken an  
445 inventory of the different strategies, depending on the geographical zone. Despite the  
446 perceived efficiency of all of these substances, we cannot ignore the constraints on use,  
447 environmental risk, human health and toxicity to non-target organisms (Pluke et al. 1999;  
448 Clausen and Yang 2007; Santana et al. 2010; Scheffrahn and Scherer 2013; Scheffrahn et al.  
449 2014). However, the efficacy of the different strategies mentioned above is mainly evaluated  
450 against subterranean termite species. Despite their recognized status as a significant urban  
451 pest, few references specifically mention arboreal termites, particularly *Nasutitermes* spp.  
452 This observation can be explained by several factors. First, damages caused by subterranean  
453 termites are less predictable, and preventive treatments must therefore be very efficient and  
454 are crucially needed. In fact, in regard to physical management, the easily detected *N.*  
455 *corniger* nests are often simply collected, broken and/or burnt (UNEP 2000; Pluke et al.  
456 1999), whereas barriers often containing insecticides must be used as a management strategy  
457 for subterranean termites (Verma et al. 2009; UNEP 2000; Paiva et al. 2011). A second factor  
458 to be taken into account is the fact that *Nasutitermes* species mostly impact Central and South  
459 America, alongside other tropical zones of the globe, such as Southeast Asia and Australia,  
460 while the main commercial markets related to insecticidal products are located in the  
461 Northern hemisphere, mostly concerned with subterranean termites (Constantino et al. 2002;

462 UNEP 2000; Miura et al. 2000). For example, in 2008, North America represented 60% of  
463 the total market for wood preserving biocides and Europe and Asia/Oceania represented 20%  
464 each (Schultz et al. 2008).

465 However, products for wood protection commercially available in the market must be  
466 active against a wide range of organisms, from decaying fungi to various xylophagous insects  
467 (Schultz et al. 2007). Even if species specificities exist, the insecticidal products mainly tested  
468 on subterranean termites (which target the workers caste) are thus also efficient towards  
469 arboreal termites, such as *N. corniger*. In the following sections, we thus focused as much as  
470 possible on environmentally low-risk management strategies, presenting examples  
471 specifically concerning *N. corniger* but also some references concerning *Nasutitermes* sp. and  
472 sometimes about other termites species when needed.

473

#### 474 **Botanical insecticides: antitermitic extracts and compounds**

475 Numerous laboratory studies target the evaluation of botanical extracts and natural  
476 compounds against termites. Even if they mostly address the activity of these products against  
477 subterranean species, some interesting results can be cited concerning *Nasutitermes* spp. and,  
478 more particularly *N. corniger*.

479 One strategy for finding new specific termiticidal compounds from botanical sources  
480 is called “bioinspiration,” which aims to understand the functional role of secondary  
481 metabolites in living organisms, thus gaining inspiration from the abilities of plants or  
482 microorganisms to produce adapted bioactive molecules under specific environmental  
483 conditions (Rodrigues et al. 2010; Basset et al. 2012; Houël et al. 2015). In particular, one  
484 source for these antitermitic natural compounds are woods naturally resistant to  
485 biodegradation, which is closely linked to the accumulation of extractives typically in the  
486 heartwood (Taylor et al. 2002; Ragon et al. 2008; Kampe and Magel 2013). Results

487 concerning wood extracts activity against *N. corniger* or *Nasutitermes* sp. (Peres Filho et al.  
488 2006; Barbosa et al. 2007; Sá et al. 2008; 2009; Santana et al. 2010; Boulogne et al. 2011;  
489 Rodrigues et al. 2011; Rodrigues et al. 2010) are summed up in Table 2.

490 The research for natural extracts for wood protection contemplates various modes of  
491 action such as elicitors, regulators, inhibitors, enzymes, or repellents for pest control. In fact,  
492 specific defense mechanisms were evidenced in plant seeds and roots, which are essential for  
493 the propagation and survival of the species. Lectins, for example, which are toxic proteins  
494 widely distributed among plants, are supposedly involved in defense mechanisms against  
495 phytophagous predators (Carlini and Grossi 2002). These compounds, isolated from various  
496 sources, were extensively studied for their insecticidal activity, *N. corniger* being among the  
497 selected targets (Sá et al. 2008; Silva et al. 2009; Napoleão et al. 2011; Paiva et al. 2011;  
498 Souza et al. 2011). These proteins play a role in cell agglutination by carbohydrate  
499 recognition and could therefore act by binding to glycoproteins present in the insect's  
500 digestive tract (Sá et al. 2008). They were demonstrated to be able to disrupt enzymes'  
501 activities from the gut of termites (Lima et al. 2014). These molecules are now the basis of  
502 commercial formulations currently developed against termites (Paiva et al. 2011). Eventually,  
503 some well-known insecticidal compounds from plant extracts are active as biocides, strong  
504 repellants or antifeedants against several species, including subterranean termites (Sharma et  
505 al. 1991; Grace and Yates 1992; Serit et al. 1992; Ivbijaro 1993; Delate and Grace 1995;  
506 Chuanchuan et al. 1998; UNEP 2000; YunLing et al. 2009; Tahiri et al. 2011; Sharma et al.  
507 2011; Himmi et al. 2013; Boulogne et al. In prep.) (Table 2).

508 Concurrently to the evaluation of extracts' biological activity, several reviews have  
509 been reported in natural products for wood protection (Singh and Singh 2012; Verma et al.  
510 2009; Yang 2009; Mai et al. 2004; Kirker et al. 2013; González-Laredo et al. 2015). These  
511 reports discuss the development of botanical pesticides against subterranean termites, with in

512 particular results concerning *Nasutitermes* wood decay control. Some extracts could be  
513 employed unadjuvanted as wood protectants, as reported in an African study, about the  
514 effective extracts of *Erythrophleum suaveolens* (Guill. & Perr.) Brenan (Fabaceae),  
515 *Azadirachta indica* A. Juss. (Meliaceae) and *Chromolaena odorata* (L.) King & Rob.  
516 (Asteraceae) in improving the durability of *Antiaris toxicaria* Lesch. (Moraceae) wood,  
517 exposed to decay for five years (Antwi-Boasiako and Damoah, 2010). In another study,  
518 *Cryptomeria japonica* (Thunb. ex L. f.) D. Don (Cupressaceae) wood treated with essential  
519 oils, showed strong activity against subterranean termites, in a three weeks test (Kartal *et al.*,  
520 2006). Turner and Conradie have also demonstrated the enhanced termitic resistance of *Pinus*  
521 *patula* Schltdl. & Cham. (Pinaceae) treated with extracts from four African durable species -  
522 *Breonadia salicina* (Vahl) Hepper & Wood (Rubiaceae), *Spirostachys Africana* Sond.  
523 (Euphorbiaceae), *Ptaeroxylon obliquum* (Thunb.) Radlk. (Rutaceae) and *Syncarpia*  
524 *glomulifera* (Sm.) Nied. (Myrtaceae)- in a two years test (Turner and Conradie, 1995).

525 Another way to employ botanical pesticides is to combine natural products to other  
526 protectants compounds, such as described in a 2007 study, where 0.5 percent thujaplicin was  
527 used in several multicomponent biocide systems with borate and carbon-based biocides.  
528 Noticeable results were obtained for protecting wood from mold, decay, and termite damage  
529 (Clausen and Yang 2007).

530 Despite all these advances, until now there has been no available chemical formulation  
531 containing these compounds for wood treatment against termites. Moreover, although they  
532 present a repulsive effect against *N. corniger*, their effects are not persistent and they did not  
533 lead to any contact toxicity (Paes et al. 2010).

534

535 **Botanical insecticides: antimicrobial extracts and compounds**

536 In most previously cited studies, the authors chose to use bioassays using the whole  
537 insect as a target, thus highlighting potent extracts or molecules. However, another process  
538 could be used to precisely search for compounds or extracts acting on a selected mechanism  
539 of action, as exemplified by Bulmer et al. (2009) with the glycomimetic molecule D- $\delta$ -  
540 gluconolactone, as above cited in this review. Thus, in-depth studies of *N. corniger* biology  
541 could be helpful for the discovery of targeted alternatives to non-specific pesticides.

542 Another specific approach based on natural processes is searching for phytochemicals  
543 targeting termites bacterial gut community. Even if some publications describe antimicrobial  
544 activities of compounds isolated from *Nasutitermes* sp. (Zhao et al. 2004; Siderhurst et al.  
545 2005; Coutinho et al. 2009; Coutinho et al. 2010; Nirma et al. 2013), few articles describe the  
546 search for antibacterial products according to the perspective of an integrated pest  
547 management strategy against *Nasutitermes* species. However, a recent study showed that  
548 botanical lectins had an antibacterial effect on symbiotic bacteria from the gut of *N. corniger*  
549 (Napoleão et al. 2011). This approach could be of valuable interest, as similar results have  
550 also been achieved with other termite species (Table 2) (Maistrello et al. 2001; Maistrello et  
551 al. 2003; Ahmed et al. 2006; Doolittle et al. 2007).

552

### 553 **Other biopesticides**

554 Other strategy for finding new termiticidal compounds from other sources is  
555 considering soil actinomycetes fermentation products. These naturally occurring compounds  
556 were discovered from *Streptomyces* sp. culture broths. Some studies dealt with control of  
557 termites with these pesticides. Indeed, Chen et al. (2015) found that avermectin (abamectin  
558 and ivermectin) has optimal insecticidal properties to manage the subterranean termite  
559 *Reticulitermes speratus*. This strategy could be tested in the control of *Nasutitermes* but it has  
560 to be taken into account that these compounds have a large range of action and thus



561 potentially noticeable impact in the field, being used in particular as an agent against worms,  
562 ticks, flies and other insects in veterinary applications (Duke et al. 2010).

563

#### 564 **Biological control of termites: entomopathogens and natural enemies**

565 Nematodes, bacteria, and fungi have several interesting properties for the biological  
566 control of termites (Verma et al. 2009; Paiva et al. 2011). In recent years, the number of  
567 publications concerning the biological control of termites has increased dramatically  
568 (Chouvenc et al. 2011). In a critical review based on the study of 227 publications in which  
569 427 bioassays were reported, Chouvenc et al. (2011) showed that these strategies were largely  
570 unsuccessful. Even if numerous examples of bacterial and nematode control can be found in  
571 the recent literature, mostly concerning subterranean termites (Grewal et al. 1999; Mo et al.  
572 2006; Devi et al. 2007; Verma et al. 2009; Chouvenc et al. 2011), the authors raise questions  
573 about the fact that the described protocols may encounter poor biological relevancy, that the  
574 obtained data may often be improperly and overly optimistically interpreted, and that field  
575 bioassays often lack (Chouvenc et al. 2011). Other reasons that potentially explain this  
576 lacking of success may be linked to the remarkable way that termites have evolved to resist  
577 diseases due to biochemical and immunological strategies (Meikle et al. 2005), as also  
578 exemplified earlier in this review.

579 Among the few successes, biological control using fungi against *Nasutitermes* sp.  
580 (Table 2) should be mentioned (Ensaf et al. 2006; Chouvenc et al. 2011; Salas-Acuña 2012).  
581 A commercial formulation using the generalist entomopathogenic fungus *Metarhizium*  
582 *anisopliae* (formerly flavoviride) (Metsch.) Sorokin (Bioblast<sup>TM</sup>, Ecoscience Co.) was  
583 developed, but was unfortunately removed from the market in the early 2000s due to  
584 insufficient results (Verma et al. 2009; Chouvenc et al. 2011). The pathogenicity of the  
585 fungus is dependent on various factors, such as its capacity for germination and penetration

586 on and through the cuticle as well as the insect's immune system to prevent fungus growth  
587 (Verma et al. 2009). A perspective to improve the efficacy of this enthomopathogen would  
588 therefore be to collect strains directly from native infected termites to improve the probability  
589 of isolating fungi having circumvented termites' adaptation strategies and natural defenses  
590 (Meikle et al. 2005). The challenge in termites' biological control is thus to develop more  
591 biologically relevant models, promote interdisciplinarity to finalize and conduct the assays,  
592 and add field and technology transfer studies (Chouvenc et al. 2011). As described earlier in  
593 their review, Chouvenc et al. (2011) also clearly appeal to an increase in research concerning  
594 termites' biology to find ways for pathogens to bypass termites' defense mechanisms.

595 In addition to entomopathogens, other biological control agents may involve some  
596 predators like ants, such as *Camponotus abdominalis*, one of the most aggressive species of  
597 this fierce natural enemy of termites (UNEP 2000). Another well-known predator of *N.*  
598 *corniger* is the hemipteran *Salyavata variegata* nymph (Reduviidae), which captures termite  
599 workers with the help of traps made of empty carcasses of previous prey and carton crumbs  
600 (McMahan 1982). However, the investigation of natural predators as control agents did not  
601 reveal any commercial potential (Chouvenc et al. 2011).

602

### 603 **3.3 Not only a pest!**

604 As with other termite species, *N. corniger* is a decomposer insect that plays a  
605 fundamental role in the decomposition process and nutrient cycling by aerating the soil,  
606 recycling plant matter and fixing nitrogen (Vasconcellos and Moura 2010). The presence of  
607 these insects also indicates the good health of an ecosystem, and they can be considered as  
608 bioindicators of its actual function (Täyasu et al. 1994; Paiva et al. 2011). Moreover, the  
609 presence of termites has a positive impact on biodiversity, termitariophile organisms, or  
610 insects depending on the nest structure for shelter, food or reproduction, thus being

611 maintained in the environment (Jaffe et al. 1995; Santos et al. 2010). Eventually, arboreal  
612 nests may also provide homes for other animals, such as birds and bats (Postava-Davignon et  
613 al. 2010).

614 Concurrently with playing a role in dynamic environmental processes, *N. corniger* can  
615 also provide services to mankind, acting as a source of active secondary metabolites,  
616 particularly antimicrobial compounds. Inspired from its traditional use as a medicine in  
617 Northeastern Brazil, aqueous extracts from *N. corniger* were studied and shown to exhibit low  
618 antimicrobial activity against *Escherichia coli* aminoglycoside-resistant strains, but presented  
619 interesting synergist activities with antibiotics (Coutinho et al. 2009; 2010). Extracts from *N.*  
620 *corniger* could therefore be used as sources of compounds to bypass bacterial resistance  
621 mechanisms. Other results highlighted antibacterial (Zhao et al. 2004) or antifungal (Bulmer  
622 and Crozier 2004) activities for compounds isolated from *Nasutitermes* species. Eventually,  
623 active compounds can also be obtained through termites' symbionts, such as the antifungal  
624 compounds tyroscherin and N-methyltyroscherin, isolated from *Pseudallescheria boydii*, a  
625 saprophytic fungus frequently found in soil and water, but that was isolated in this case from  
626 *Nasutitermes* sp. (Nirma et al. 2013). In addition to appealing to the preservation and the  
627 pharmacochemical study of this species, these examples highlight the fact that improving the  
628 knowledge of termites, and more particularly *N. corniger* biology, could lead to a marked  
629 improvement, not only in the pest management field but also in the continuous search for new  
630 antimicrobial compounds.

631

#### 632 **4. Conclusion**

633 *Nasutitermes* is the most species-rich termite genus, with a complex taxonomic  
634 history, and a growing number of known species present in all biogeographical regions.  
635 *Nasutitermes corniger*, which is the type-species of the genus, is an urban and agricultural

636 pest, and also an invasive species, with a remarkable ability to adapt to a variety of habitats  
637 and food sources. Controversially, ecological and human health problems potentially arising  
638 from the use of synthetic chemical substances, particularly if the label guidelines are not  
639 strictly followed, are the limiting factor for their use. However, the extensive use of botanical  
640 or biological insecticides remains up to date inconclusive because of their ineffectiveness or  
641 their poor durability in external wood exposure cases. In the continuous effort to develop safe  
642 and effective methods for conehead termite management, we therefore believe that a  
643 paradigm shift is necessary and that sustained efforts must be performed in the field of termite  
644 biology. Alongside an increase in field bioassays, improvement in this knowledge is the key  
645 to more elaborate pertinent models and integrated strategies, targeting both the insect and its  
646 symbionts.

647       Eventually, integrated management rather than eradication is necessary in the native  
648 zones of occurrence of this termite. Although it is considered to be a pest, the termite is  
649 clearly an essential component of ecosystems as well as a potential source of valuable  
650 compounds that could contribute to the improvement of human health. Thus, the perspective  
651 remains open concerning *Nasutitermes* species study and management, and exciting  
652 discoveries are still to be made.

653

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662

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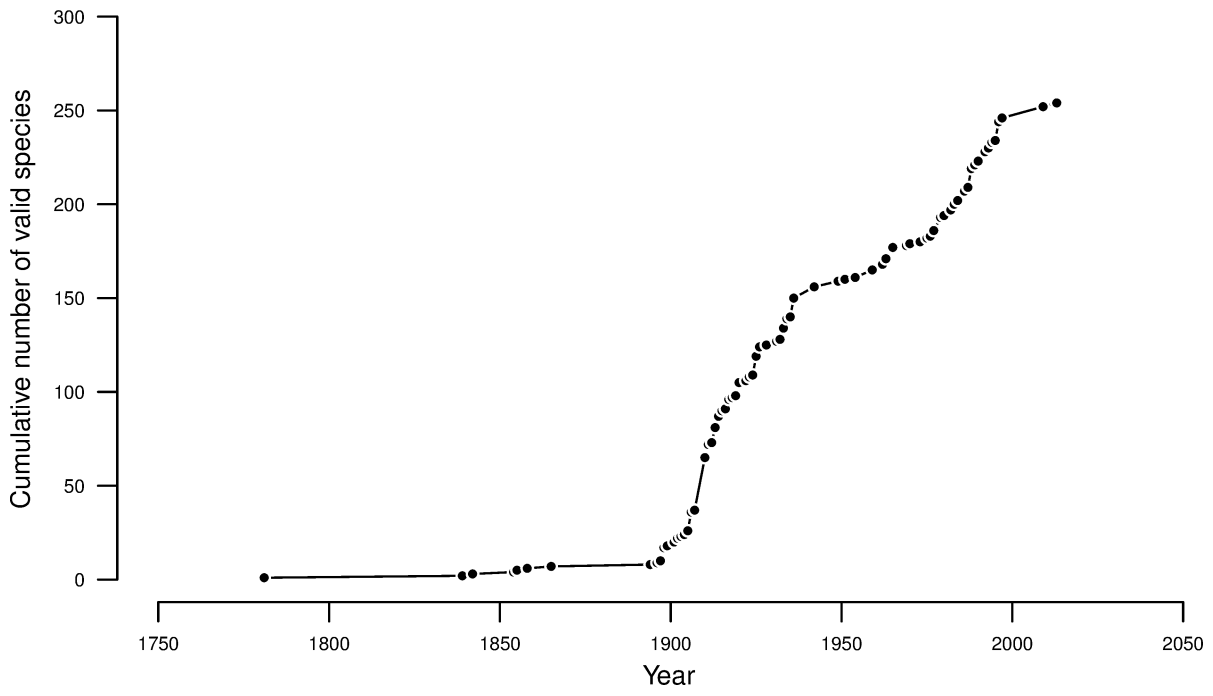
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**Figure 1:** Cumulative number of valid species of *Nasutitermes* since 1758.



**Figure 2:** Geographical distribution of *Nasutitermes corniger*. This termite is native of Central and South America and the Caribbean islands, and is invasive in the Bahamas, Florida and New Guinea (according to Scheffrahn et al. and Evans et al.).<sup>7,9</sup>

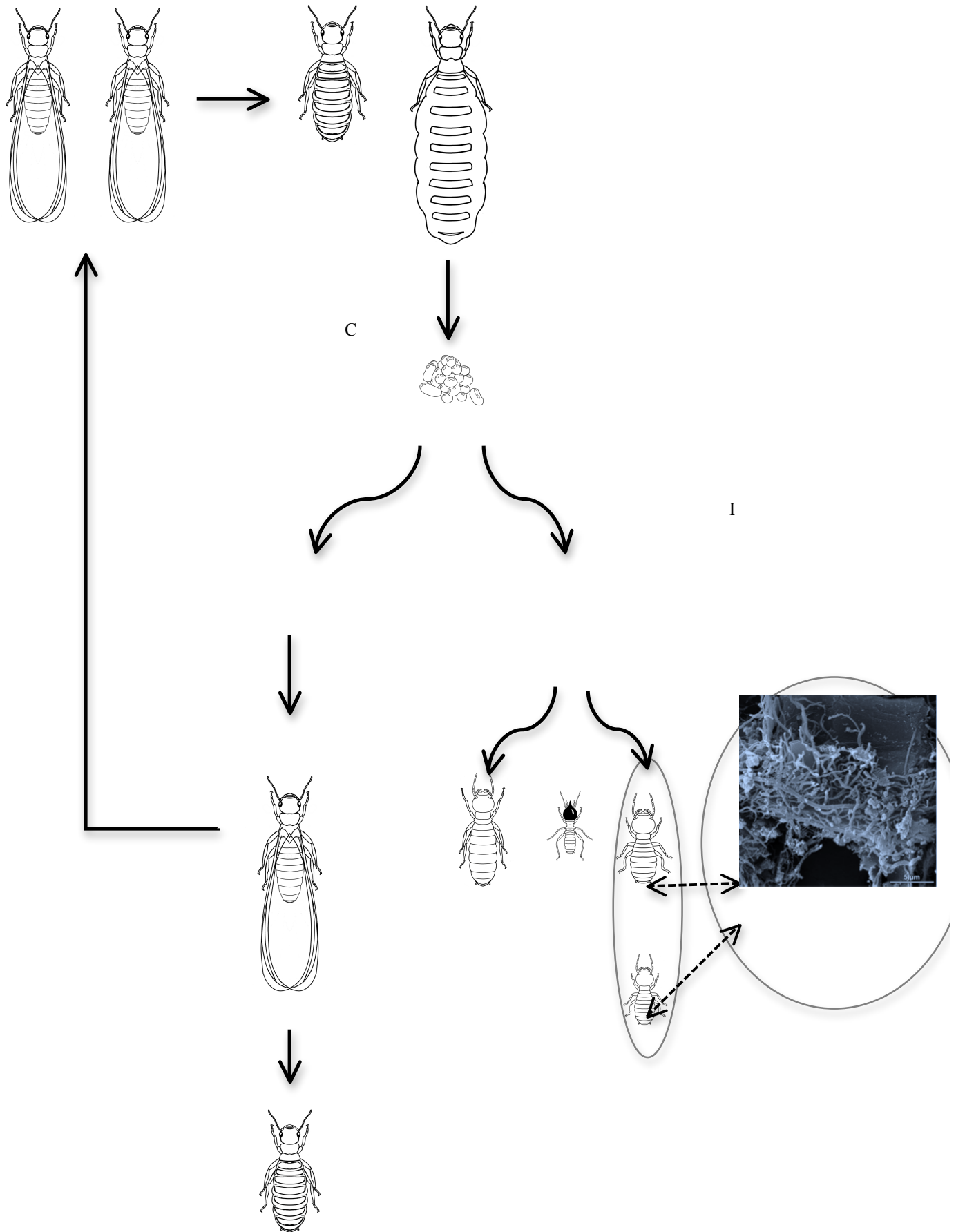


♂  
Nymphal (Imaginal) line

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♀  
Apterous line

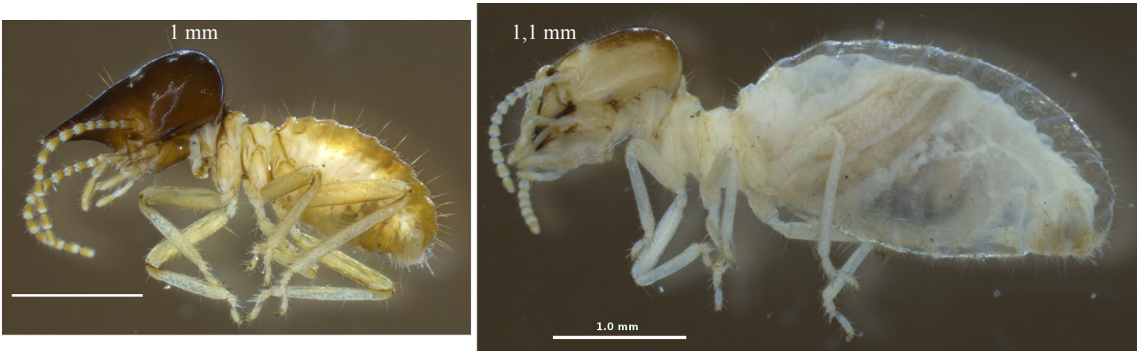
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**Figure 3:** *Nasutitermes corniger*'s colony with the king (A), queen (B), eggs (C), alate (D), adultoid (E), ergatoid (F), large (G1) and small (G2) workers, soldier (H), and gut's microbiome (photo according to Mikaelyan et al. 2014) (I).

Dotted arrows indicate symbiotic relationships. Gray circles indicate targets of all pest management strategies found in the literature.

**Figure 4:** Soldier (left) and major worker (right) of *Nasutitermes corniger*, same magnification. © Copyright 2016 R. Constantino.



**Figure 5:** Arboreal nest of *Nasutitermes corniger* on a cacao tree. © Copyright 2016 R. Constantino.





**Table 1:** Examples of the synthetic chemical products used for termite management.

Classes	Active compounds	References
Arsenic derivatives	Chromated copper arsenate (CCA) Arsenic trioxide Calcium arsenate	Schultz et al. 2007  Verma et al. 2009; UNEP 2000; Santana et al. 2010
Copper derivatives	Alkaline copper quat (ACQ) Copper azole Copper naphthenate	UNEP 2000; Schultz et al. 2007
Zinc derivatives	Zinc naphthenate	UNEP 2000; Schultz et al. 2007
Borate formulations	Disodium octaborate tetrahydrate (DOT)	UNEP 2000; Schultz et al. 2007; Clausen and Yang 2007
Pyrethroids	Permethrin	UNEP 2000; Schultz et al. 2007
Neonicotinoids	Imidacloprid Thiamethoxan	Schultz et al. 2007; Scheffrahn et al. 2014
Phenylpyrazoles	Fipronil,  Chlorfenapyr	Verma et al. 2009; UNEP 2000; Scheffrahn et al. 2014, Santana et al. 2010
Pyrethroid ethers	Silafluofen	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Organophosphate compounds	Chlorpyrifos Fenitrothion Phenthoate Triazophos	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Organochlorate compounds	Chlorothalonil	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Benzoylureas	Chlorfluazuron Diflubenzuron Hexaflumuron Triflumuron	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Anthralinic diamides	Chlorantraniliprole	Verma et al. 2009; UNEP 2000; Santana et al. 2010; Scheffrahn and Scherer 2013
Aminohydrazones	Hydramethylnon	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Spinosoids	Spinosad	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Sulfonamides	Sulfluramid	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Organic and inorganic gas	Carbon dioxide Methyl bromide Phosphine Sulfuryl fluoride	Verma et al. 2009; UNEP 2000; Santana et al. 2010; Scheffrahn et al. 2014

**Table 2:** Sustainable management with antitermitic and antimicrobial botanicals and with entomopathogens.

Termite	Plant (Family)/part of plant or Entomopathogens (Family)	Activity	Active extracts / compounds	References
<b>Antitermitic botanicals</b>				
<i>N. corniger</i>	<i>Diospyros dichroa</i> Sandw. (Ebenaceae)	Repellent activity (> 90%) at 3.2 µg/mm <sup>2</sup> (40 mg/ml)	Wood ethyl acetate extract	Pers. results based on Ganapaty et al 2004, Rodrigues 2010, and Boulogne et al 2011 previous works
<i>N. corniger</i>	<i>Lonchocarpus chrysophyllus</i> Kleinhoonte (Fabaceae)	Repellent activity (> 90%) at 3.2 µg/mm <sup>2</sup> (40 mg/ml)	Bark ethyl acetate and petroleum ether extracts	Pers. results (Boulogne et al. <i>in prep</i> )
<i>N. corniger</i>	<i>Myracrodruon urundeuwa</i> Allemão (Anacardiaceae)/ heartwood	No repellent activity Contact toxicity (LC <sub>50</sub> =0.248 mg/mL for workers and 0.199 mg/mL for soldiers)	Lectins	Sá et al. 2008
<i>N. corniger</i>	<i>Myracrodruon urundeuwa</i> Allemão (Anacardiaceae)/ heartwood and bark	No contact toxicity Repellent activity	Crude methanolic extract	Sá et al. 2009
<i>N. corniger</i>	<i>Anadenanthera colubrina</i> (Vell.) Brenan (Fabaceae)/ heartwood	Contact toxicity (LC <sub>50</sub> = 7.3 mg/mL for ethyl acetate extract, LC <sub>50</sub> = 67.4 mg/mL for cyclohexane extract after 4 days)	Cyclohexane and ethyl acetate extracts	Santana et al. 2010
<i>N. corniger</i>	<i>Hymenaea stigonocarpa</i> Hayne (Fabaceae)/ heartwood	Contact toxicity (LC <sub>50</sub> =11.9 mg/mL after 4 days)	Cyclohexane extract	Santana et al. 2010
<i>N. corniger</i>	<i>Bowdichia virgilioides</i> Kunth, (Fabaceae)/ heartwood	Contact toxicity (LC <sub>50</sub> =7.2 mg/mL after 4 days)	Alkaloidal extract	Santana et al. 2010
<i>N. corniger</i>	<i>Bowdichia virgilioides</i> Kunth, (Fabaceae)/ heartwood	Toxic (LC <sub>50</sub> =12.2 mg/mL after 4 days) and repellent activities	Cyclohexane extract	Santana et al. 2010
<i>N. macrocephalus</i>	<i>Sextonia rubra</i> (Mez) Van der Werff (Lauraceae)/ heartwood	Contact toxicity (LC <sub>100</sub> <1.9 µg/mm <sup>2</sup> after 72h)	Ethyl-acetate extract/ rubrynolide	Rodrigues et al. 2011
<i>Nasutitermes</i> sp	<i>Bagassa guianensis</i> Aubl. (Moraceae), <i>Erismia uncinatum</i> Warm. (Vochysiaceae), <i>Buchenavia parvifolia</i> Ducke (Combretaceae), <i>Dinizia excelsa</i> Ducke (Fabaceae) <i>Pouteria guianensis</i> Aubl. (Sapotaceae)/ wood	Wood impregnation conferred durability to <i>Cecropia</i> sp. (Urticaceae) and <i>Simarouba amara</i> Aubl. (Simaroubaceae) woods		Barbosa et al. 2007; Peres Filho et al. 2006
<i>N. macrocephalus</i>	<i>Diospyros dichroa</i> Sandw. (Ebenaceae)/ wood	Contact toxicity (LC <sub>100</sub> <1.9 µg/mm <sup>2</sup> and 5.6 µg/mm <sup>2</sup> after 72h)	Methanolic extract and Ethyl acetate extract.	Harun and Labosky 1985; Rodrigues 2010
<i>N. corniger</i>	<i>Bauhinia monandra</i> Kurz (Fabaceae)/ roots	Contact toxicity (LC <sub>50</sub> = 0.09 mg/mL for workers and 0.395 for soldiers after 12 days)	Lectins	Souza et al. 2011
<i>N. corniger</i>	<i>Opuntia ficus-indica</i> (L.) Mill. (Cactaceae)/ cladodes	Contact toxicity (LC <sub>50</sub> =0.116 mg/mL for workers and 1.5 for soldiers)	Lectins	Paiva et al. 2011
<i>N. corniger</i>	<i>Moringa oleifera</i> Lam. (Moringaceae)/ seeds	No repellent activity Contact toxicity at 1.0 and 1.5 mg/mL	Lectins	Paiva et al. 2011
<i>N. corniger</i>	<i>Myracrodruon urundeuwa</i> Allemão (Anacardiaceae)/ leaves	Contact toxicity (LC <sub>50</sub> =0.374 to 0.974 mg/ml on workers and 0.432 to 0.787 mg/ml on soldiers)	Lectins	Napoleão et al. 2011
<i>N. corniger</i>	<i>Cladonia verticillaris</i>	Contact toxicity	Lectins	Silva et al. 2009

	(Cladoniaceae) / lichen	(LC <sub>50</sub> = 0.196 mg/mL on workers and 0.5 mg/mL on soldiers after 10 days)		
<i>N. corniger</i>	<i>Microgramma vaccinifolia</i> (Langsd. & Fisch.) Copel. (Polypodiaceae)/ rhizome	Contact toxicity Ability to disrupt trypsin-like protease, acid phosphatase, and cellulase activities in termite's gut	Lectins	Lima et al. 2014
<i>Coptotermes formosanus</i> , <i>Coptotermes gestroi</i> , <i>Reticulitermes speratus</i> , <i>Macrotermes bellicosus</i> , <i>Macrotermes nigeriensis</i> , <i>Odontotermes obesus</i> ,	<i>Azadirachta indica</i> A. Juss. (Meliaceae)  <i>Ricinus communis</i> L. (Euphorbiaceae)	Contact toxicity , metabolic poison, repellent or antifeedant activities		Sharma et al. 1991; Grace and Yates 1992; Serit et al. 1992; Ivbijaro et al. 1993; Delate and Grace 1995; Chuanchuan et al. 1998; UNEP 2000; Yunling et al. 2009; Sharma et al. 2011; Tahiri et al. 2011; Himmi et al. 2013
<b>Antimicrobial botanicals</b>				
<i>N. corniger</i>	<i>Myracrodruon urundeuva</i> Allemão (Anacardiaceae)/ bark, heartwood and leaf	Antibacterial activity on gut's symbiotic bacteria (MIC from 62.5 to 250 mg/mL)	Lectins	Napoleão et al. 2011
<i>Microtermes obesi</i>	<i>Withania somnifera</i> (L.) Dunal (Solanaceae), <i>Croton tiglium</i> L. (Euphorbiaceae) and <i>Hygrophila auriculata</i> Schumach.) Heine (Acanthaceae) / seeds and leaves	Reduction of colonies number of bacterial symbionts		Ahmed et al. 2006
<i>Coptotermes formosanus</i>	<i>Chrysopogon zizanioides</i> (L.) <i>Roberty</i> (syn. <i>Vetiveria zizanioides</i> (L.) Nash) (Poaceae)	Reduction number of hindgut flagellate species (more specially <i>Pseudotriconympha grassii</i> , an important cellulolytic flagellate protist)	Oil/ Nootkatone	Maistrello et al. 2003; 2011
<i>Coptotermes formosanus</i>	<i>Azadirachta indica</i> A. Juss. (Meliaceae)	Reduction of population of <i>P. grassii</i> and <i>Spirochaetes</i>	Azadirachtin	Doolittle et al. 2007
<b>Entomopatogens</b>				
<i>Nasutitermes</i> sp.	<i>Termitaria coronata</i> (Deuteromycetes, Termitariales)			Ensaf et al. 2006
<i>N. corniger</i> and <i>Nasutitermes</i> sp.	<i>Metarhizium</i> sp			Chouvenec et al. 2011; Salas-Acuña 2012