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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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28

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 19th 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 19th 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 20th
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 H₂ generation and CO₂-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 *Cellulomonodaceae*, *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* Schltldl. & 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- δ -
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 (BioblastTM, 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 entomopathogen 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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Figure 1: Cumulative number of valid species of *Nasutitermes* since 1758.

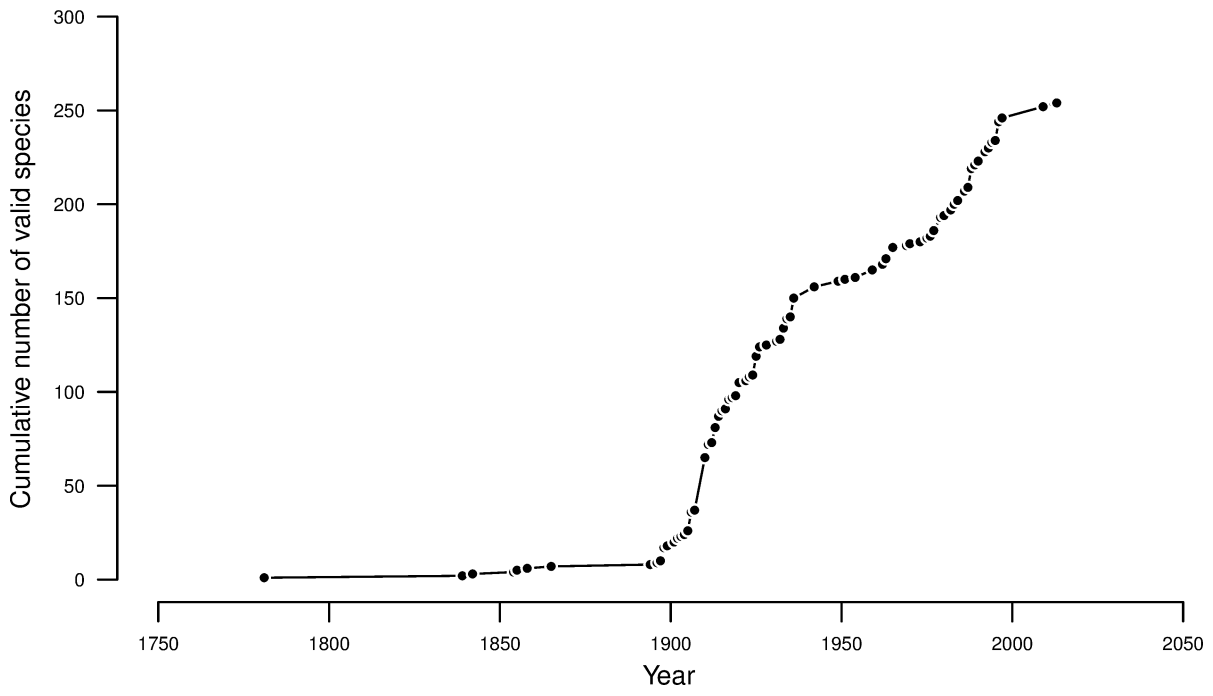


Figure 2: Geographical distribution of *Nasutitermes corniger*. This termite is native of Central and South America and the Caribbean islands, and is invasive in the Bahamas, Florida and New Guinea (according to Scheffrahn et al. and Evans et al.).^{7,9}



♂
Nymphal (Imaginal) line

r

♀
Apterous line

G2

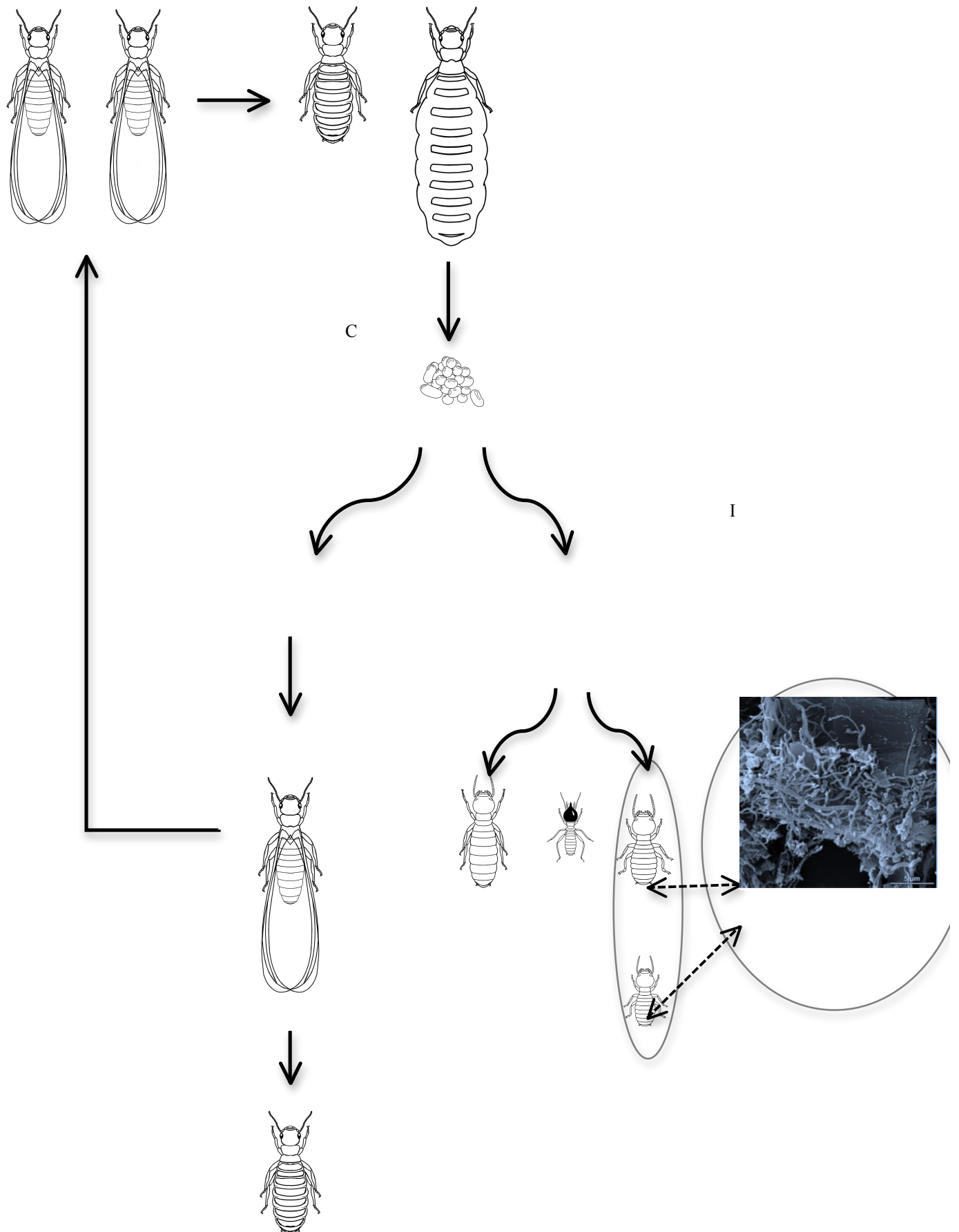


Figure 3: *Nasutitermes corniger*'s colony with the king (A), queen (B), eggs (C), alate (D), adultoid (E), ergatoid (F), large (G1) and small (G2) workers, soldier (H), and gut's microbiome (photo according to Mikaelyan et al. 2014) (I).

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.

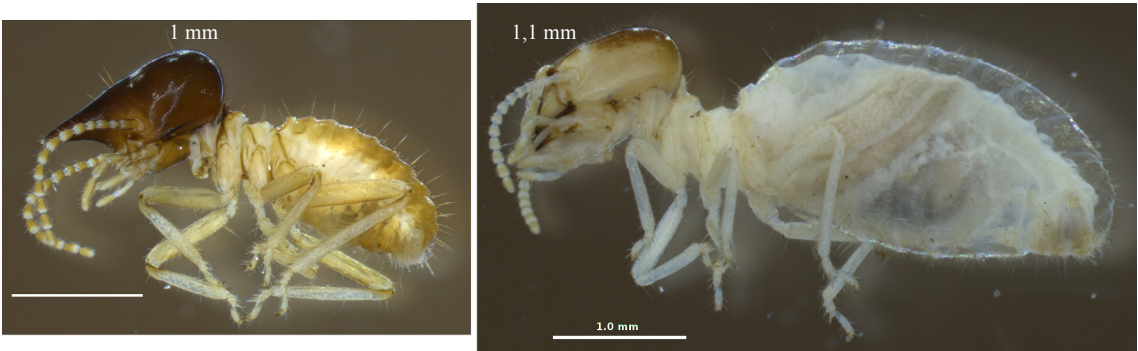


Figure 5: Arboreal nest of *Nasutitermes corniger* on a cacao tree. © Copyright 2016 R. Constantino.



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
Antitermitic botanicals				
<i>N. corniger</i>	<i>Diospyros dichroa</i> Sandw. (Ebenaceae)	Repellent activity (> 90%) at 3.2 µg/mm ² (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 ² (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 ₅₀ =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 ₅₀ = 7.3 mg/mL for ethyl acetate extract, LC ₅₀ = 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 ₅₀ =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 ₅₀ =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 ₅₀ =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 ₁₀₀ <1.9 µg/mm ² 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 ₁₀₀ <1.9 µg/mm ² and 5.6 µg/mm ² 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 ₅₀ = 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 ₅₀ =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 ₅₀ =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 ₅₀ = 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
Antimicrobial botanicals				
<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>Pseudotrichonympha 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
Entomopatogens				
<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