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

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2   **potential for science-based development of sustainable pest management programs**

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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

Abstract

46

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.

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1. Introduction

65

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 heterogeneus 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 Cuezzo 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, β(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

15

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_2 generation and CO_2-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 maker 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. takasagoenis* 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

3.2 Pest management

Synthetic chemical products, as active substances inhibiting wood degradation by termites

and microorganisms, can be applied through soil, wood treatment, or chemical fumigations,

before or after infestation (Paiva et al. 2011) (Table 1). Excellent reviews or technical reports,

such as those by Schultz et al. (2007; 2008) concerning wood preservation, Verma et al.

(2009) on the biological control of termites, or the expert group on termite biology and

management of the United Nations Environment Program (UNEP 2000), have taken an

inventory of the different strategies, depending on the geographical zone. Despite the

perceived efficiency of all of these substances, we cannot ignore the constraints on use,

environmental risk, human health and toxicity to non-target organisms (Pluke et al. 1999;

Clausen and Yang 2007; Santana et al. 2010; Scheffrahn and Scherer 2013; Scheffrahn et al.

2014). However, the efficacy of the different strategies mentioned above is mainly evaluated

against subterranean termite species. Despite their recognized status as a significant urban

pest, few references specifically mention arboreal termites, particularly *Nasutitermes* spp.

This observation can be explained by several factors. First, damages caused by subterranean

termites are less predictable, and preventive treatments must therefore be very efficient and

are crucially needed. In fact, in regard to physical management, the easily detected *N.*

corniger nests are often simply collected, broken and/or burnt (UNEP 2000; Pluke et al.

1999), whereas barriers often containing insecticides must be used as a management strategy

for subterranean termites (Verma et al. 2009; UNEP 2000; Paiva et al. 2011). A second factor

to be taken into account is the fact that *Nasutitermes* species mostly impact Central and South

America, alongside other tropical zones of the globe, such as Southeast Asia and Australia,

while the main commercial markets related to insecticidal products are located in the

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-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 enthomopathogenic fungus *Metarhizium*

582   *anisopliae* (formerly flavoviride) (Metsch.) Sorokin (Bioblast[TM], 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 unconclusive 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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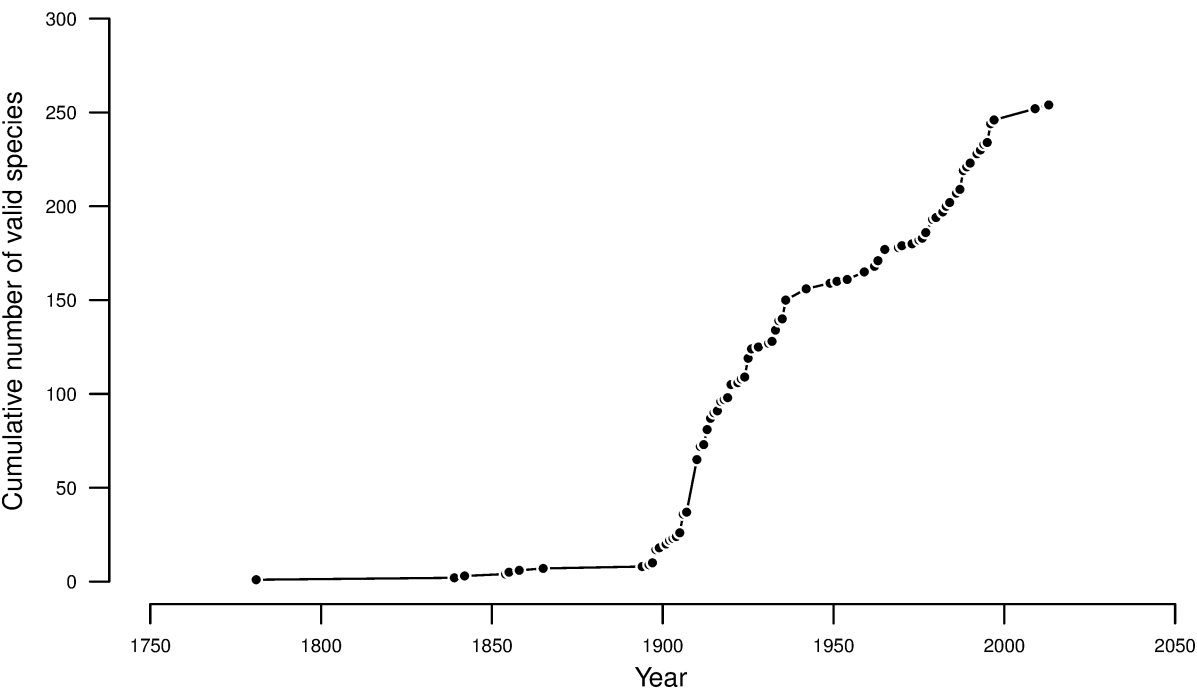**Figure 1**: Cumulative number of valid species of *Nasutitermes* since 1758.

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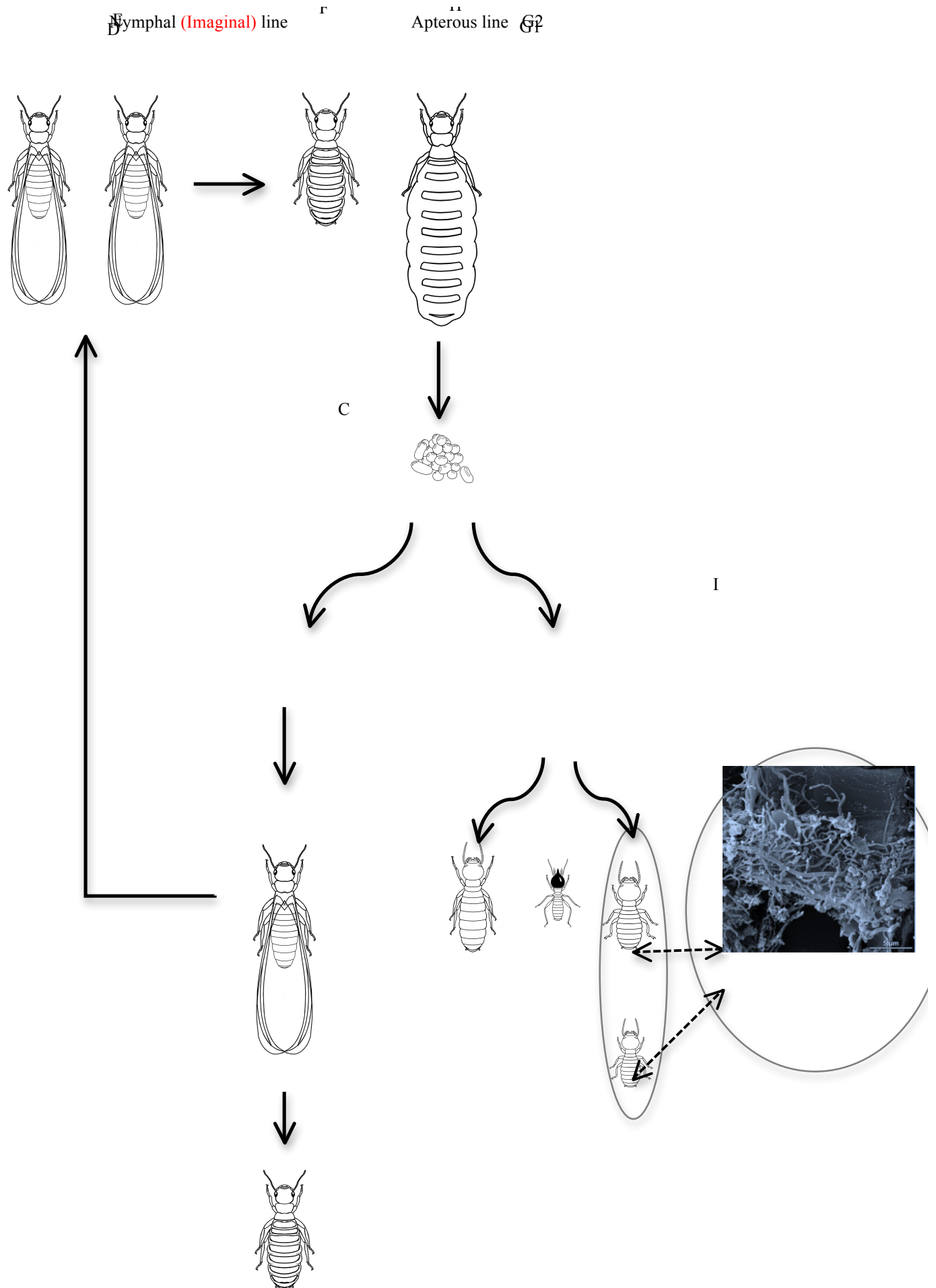
Figure 3: *Nasutitermes corniger*'s colony with the king (A), queen (B), eggs (C), alate (D), adultoid (E), ergatoid (F), large (G1) and small (G2) workers, soldier (H), and gut's microbiome (photo according to Mikaelyan et al. 2014) (I).

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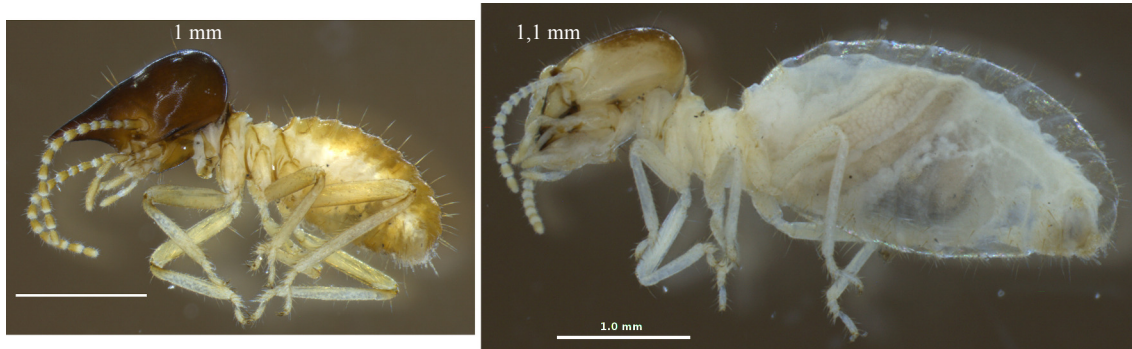
Figure 5: Arboreal nest of *Nasutitermes corniger* on a cacao tree. © Copyright 2016 R. Constantino.

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 napthenate	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		
N. corniger	*Diospyros dichroa* 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
N. corniger	*Lonchocarpus chrysophyllus 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. *in prep*)
N. corniger	*Myracrodruon urundeuva* 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
N. corniger	*M yracrodruon urundeuva* Allemão (Anacardiaceae)/ heartwood and bark	No contact toxicity Repellent activity	Crude methanolic extract	Sá et al. 2009
N. corniger	*Anadenanthera colubrina* (Vell.) Brenan (Fabaceae)/ heartwood	Contact toxicity (LC50 = 7.3 mg/mL for ethyl acetate extract , LC50 =67.4 mg/mL for cyclohexane extract after 4 days)	Cyclohexane and ethyl acetate extracts	Santana et al. 2010
N. corniger	*Hymenaea stigonocarpa* Hayne (Fabaceae)/ heartwood	Contact toxicity (LC50=11.9 mg/mL after 4 days)	Cyclohexane extract	Santana et al. 2010
N. corniger	*Bowdichia virgilioides* Kunth, (Fabaceae)/ heartwood	Contact toxicity (LC$_{50}$=7.2 mg/mL after 4 days)	Alkaloidal extract	Santana et al. 2010
N. corniger	*Bowdichia virgilioides* Kunth, (Fabaceae)/ heartwood	Toxic (LC$_{50}$=12.2 mg/mL after 4 days) and repellent activities	Cyclohexane extract	Santana et al. 2010
N. macrocephalus	*Sextonia rubra* (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
Nasutitermes sp	*Bagassa guianensis* Aubl. (Moraceae), *Erisma uncinatum* Warm. (Vochysiaceae), *Buchenavia parvifolia* Ducke (Combretaceae), *Dinizia excelsa* Ducke (Fabaceae) *Pouteria guianensis* Aubl. (Sapotaceae)/ wood	Wood impregnation conferred durability to *Cecropia* sp. (Urticaceae) and *Simarouba amara* Aubl. (Simaroubaceae) woods		Barbosa et al. 2007; Peres Filho et al. 2006
N. macrocephalus	*Diospyros dichroa* 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
N. corniger	*Bauhinia monandra* 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
N. corniger	*Opuntia ficus-indica* (L.) Mill. (Cactaceae)/ cladodes	Contact toxicity (LC$_{50}$=0.116 mg/mL for workers and 1.5 for soldiers)	Lectins	Paiva et al. 2011
N. corniger	*Moringa oleifera* Lam. (Moringaceae)/ seeds	No repellent activity Contact toxicity at 1.0 and 1.5 mg/mL	Lectins	Paiva et al. 2011
N. corniger	*Myracrodruon urundeuva* 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
N. corniger	*Cladonia verticillaris*	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)		
N. corniger	*Microgramma vaccinifolia* (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
Coptotermes formosanus, Coptotermes gestroi, Reticulitermes speratus, Macrotermes bellicosus, Macrotermes nigeriensis, Odontotermes obesus,	*Azadirachta indica* A. Juss. (Meliaceae) *Ricinus communis* 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				
N. corniger	*Myracrodruon urundeuva* 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
Microtermes obesi	*Withania somnifera* (L.) Dunal (Solanaceae)*, Croton tiglium* L. (Euphorbiaceae) and *Hygrophila auriculata* Schumach.) Heine (Acanthaceae) */* seeds and leaves	Reduction of colonies number of bacterial symbionts		Ahmed et al. 2006
Coptotermes formosanus	*Chrysopogon zizanioides* (L.) Roberty (syn.*Vetiveria zizanioides* (L.) Nash) (Poaceae)	Reduction number of hindgut flagellate species (more specially *Pseudotrichonympha grassii*, an important cellulolytic flagellate protist)	Oil/ Nootkatone	Maistrello et al. 2003; 2011
Coptotermes formosanus	*Azadirachta indica* A. Juss. (Meliaceae)	Reduction of population of *P. grassii* and *Spirochaetes*	Azadirachtin	Doolittle et al. 2007
Entomopatogens				
Nasutitermes sp.	*Termitaria coronata* (Deuteromycetes, Termitariales)			Ensaf et al. 2006
N. corniger and *Nasutitermes* sp.	*Metarhizium* sp			Chouvenc et al. 2011; Salas-Acuña 2012