

1 Termitariophily: expanding the concept of  
2 termitophily in a physogastric rove beetle  
3 (Coleoptera: Staphylinidae)

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## Abstract

1. Termitophily in some rove beetles is commonly attributed to the striking termite worker resemblance that is provided by the beetles' hypertrophic ("physogastric") abdomen. However, a termite nest may offer to a termitophile additional benefits, such as a continuously repaired shelter.
2. This sounds applicable to *Corotoca melantho* (Aleocharinae: Corotocini), a viviparous obligatory termitophile staphylinid beetle species. While conferring morphological congruence to its host worker termites, its physogastry may also impair mobility, leading to vulnerability and the need of an enclosed and secure environment. It seems plausible to hypothesise that physogastry in *Corotoca melantho* would imply in interactions between this termitophile and its host termites as well as its host termitarium.
3. Here we provide evidence to build such a hypothesis by inspecting the morpho-anatomical reproductive traits of this termitophile. We found that a gradient of growth stages of embryos and larvae in the oviduct explains physogastry in females while pointing to iteroparity. The asynchronous development of oocytes in females, combined with a full developing sequence of sperm cells indicative of continuous spermatogenesis in males, suggest frequent matings.
4. While improving guest-host similarity, physogastry and flightlessness should confer vulnerability to pregnant females, forcing *C. melantho* to seek for close and sheltered environments. These latter could facilitate male-female frequent contacts demanded by iteroparity. Physogastry in *C. melantho* could hence be thought to connect not only to the termites themselves but also to the physical structure of the termitarium. Thence, *C. melantho* can be hypothesised to be a *termitariophile* in addition to being *termitophile*.

**Keywords:** social integrative traits, termitariophily, symbiosis, social parasitism

## 37 1 Introduction

38 Termitophily is a form of symbiosis in which an arthropod invades a termite  
39 nest and establishes itself therein, cohabiting with the original termite con-  
40 structor. The advantages of such behaviour are straightforward: a continuously  
41 repaired shelter and continuously renewed resources. Not so clear-cut, however,  
42 is our understanding of the ecological and evolutionary drivers underlying such  
43 a symbiosis.

44 Invading a termite nest presents challenges, and termitophiles adopt a wide  
45 variety of strategies to gain entry. Striking integrating strategies can be found in  
46 Coleoptera: Staphylinidae (Seevers, 1957; Kistner, 1982; Howard *et al.*, 1982)  
47 and, among these beetles, *Corotoca melantho* Schiødte, 1853 (Aleocharinae:  
48 Corotocini) stands out as a prime example. Of all termitophile staphylinids pre-  
49 senting a hypertrophic (“physogastric”) abdomen, *C. melantho* is, arguably, one  
50 of the most remarkable species by its morphological congruence with the workers  
51 of its obligate termite hosts (Cunha *et al.*, 2015). On top of that, *C. melantho*  
52 individuals also share cuticular hydrocarbons with their host (Rosa *et al.*, 2018),  
53 extending to chemical traits the host-guest similarity already achieved through  
54 shape congruence.

55 These modifications are commonly interpreted as disguises to secure accep-  
56 tance for invading staphylinids as kin (Parker *et al.*, 2017). Indeed, *C. melantho*  
57 individuals are reported to engage allogrooming and trophallactic interactions  
58 with their blind worker termite hosts frequently. It seems however unwarranted  
59 to consider tactile mimicry as the sole driver of this termitophily, as the physical  
60 structure of the termitarium has also been shown to affect termitophile commu-  
61 nities (DeSouza *et al.*, 2016; Marins *et al.*, 2016; Monteiro *et al.*, 2017). Neither  
62 will it seem correct to consider physogastry as essential to host-guest intimate  
63 tactile interactions, because non-physogastric staphylinids can also engage such

64 contacts (Howard *et al.*, 1980). Other purposes of physogastry could include, for  
65 instance, disguising as a termite a guest which would otherwise be vulnerable to  
66 the non-termitophagous predators reported by de Visser *et al.* (2008) to cohabit  
67 termitaria.

68 The corollary of such evidence is that in order to understand termitophily in  
69 full, one would need to consider the dynamics occurring at the inter-individual  
70 level along with factors operating at broader levels, as proposed by Monteiro  
71 *et al.* (2017).

72 This seems particularly relevant specifically for the case of *C. melantho*.  
73 While in other termitophilous Staphylinidae physogastry has been generally  
74 associated with the hypertrophy of fat bodies (Seevers, 1957; Kistner & Pasteels,  
75 1969; Kistner, 1969; Kistner, 1990), such abdominal hypertrophy in *C. melantho*  
76 seems associated with an enlargement of sexual organs and viviparity (Kistner  
77 & Pasteels, 1969; Reichensperger, 1936).

78 This raises the question of whether termitophily and physogastry in *C.*  
79 *melantho* could have other links in addition to inter-individual interactions.  
80 After all, a mere enlargement of the abdomen via fat body accumulation (as  
81 opposed to via pregnancy) would potentially suffice as a disguise to enhance  
82 termite-beetle interactions or to defend beetles against their predators. On  
83 the other hand, by constraining mobility (Cai *et al.*, 2017) physogastry com-  
84 promises swift manoeuvring to escape predators and prolonged locomotion to  
85 find food and mates. Thus, physogastric individuals would be advantaged in a  
86 sheltered and enclosed environment where predation risks would be diminished  
87 and nutritional and mating resources, predictable. We hence hypothesise that  
88 physogastry in *C. melantho*, in addition to its role in guest-host interactions,  
89 may also be associated with the need for shelter of a pregnant viviparous female.  
90 Stated in another way, physogastry in *C. melantho* would simultaneously imply

91 in interactions between this termitophile and its host termites as well as its host  
92 termitarium.

93 Here we provide evidence to build such a hypothesis by describing the in-  
94 ternal morphology of the physogastric abdomen of *C. melantho* termitophiles,  
95 looking for modifications suggestive of roles other than social integration. Specif-  
96 ically, we focus on their physogastry as a consequence of viviparity, examining  
97 the reproductive tracts of both, males and females, as any complementarity on  
98 these would reinforce the suggestions outlined above. To the best of our knowl-  
99 edge, no previous studies have examined termitophily in *C. melantho* beyond  
100 its alleged links to tactile mimicry. We addressed such a question because of  
101 its relevance to further studies on the ecological and evolutionary purposes of  
102 termitophily. By finding any evidence for a link between these termitophiles and  
103 the physical structure of the termitarium, we will add factual evidence to early  
104 especulations by Araujo (1970). It will also contribute to the focus on abiotic  
105 factors as additional determinants of symbiosis which is gaining momentum in  
106 termitophily's contemporary research agenda (Leponce *et al.*, 1999; Cristaldo  
107 *et al.*, 2012; Marins *et al.*, 2016; DeSouza *et al.*, 2016; Monteiro *et al.*, 2017). In  
108 contrast, the absence of joint effects between biotic and abiotic factors as drivers  
109 of termitophily in these beetles could tip the ballance in favour of a completely  
110 distinct set of research questions.

## 111 **2 Material and Methods**

### 112 **2.1 Ethical statement**

113 The current study complied with relevant regulations of Brazil. This includes  
114 collecting and transportation permits from The Brazilian Institute for the Envi-  
115 ronment and Renewable Natural Resources, and permission from The Brazilian

116 Enterprise for Agricultural Research to conduct the study on their site. Tacit  
117 approval from the Brazilian Government is implied by hiring the authors as Sci-  
118 entific Researchers. No protected species was sampled. No genetic information  
119 was accessed.

## 120 **2.2 Terms definition**

121 Here we use the terms “termitarium” (plural: termitaria) or “nest” to denote  
122 the physical structure built by termites, regardless whether these are epigeal  
123 or arboreal. “Colony” denotes the assemblage of termite individuals sharing a  
124 nest and cooperating intra-specifically therein. Throughout this text, when we  
125 mention “termites” we are referring to a full colony of *Constrictotermes cypher-*  
126 *gaster* (Silvestri, 1901) (Blattodea: Isoptera: Termitidae: Nasutitermitinae). If  
127 at any point we need to refer to another termite species, we will explicitly say  
128 so.

129 “Termitophiles” are invertebrates living at least one phasis of their cycle  
130 within a termite nest. The focal termitophile species in this text is *Corotoca*  
131 *melantho* Schiødte, 1853 (Insecta: Coleoptera: Staphylinidae: Aleocharinae:  
132 Corotocini), an obligatory termitophile in the nests of *Constrictotermes cypher-*  
133 *gaster*.

134 We follow Monteiro *et al.* (2017) in using “coexistence” and “cohabitation”  
135 as synonyms to refer to the simultaneous occurrence of termites and termi-  
136 topiles within a given termitarium, without implication of reciprocal positive  
137 or negative influences. The term “intruder” may be used to refer to cohab-  
138 itants simply because they establish themselves –not necessarily by force– in  
139 nests which had not been built by/for them in the first place. Likewise, the  
140 term “guest” is used in its neutral acception of “the one who stays in another’s  
141 home” without implication of any reciprocal influences. This same neutrality is

142 assumed for the term “host”, the counterpart of “guest”.

### 143 **2.3 The termite host and its termitophile**

144 *Constrictotermes cyphergaster* is a common termite species in Brazilian savan-  
145 nas (“Cerrado”) and dry scrub (“Caatinga”). It forages in the open, in exposed  
146 columns at night, feeding on decomposing wood, tree bark, and lichens (Moura  
147 *et al.*, 2006; Bourguignon *et al.*, 2011). Colonies hold in average 4.5 workers per  
148 soldier (Cunha *et al.*, 2003), and are usually monogynic even though multiple  
149 reproductives have been already reported to occur in a few nests (Cunha &  
150 Brandão, 2002). Termitaria built by this species are initially established on the  
151 soil surface becoming arboreal as the colony matures (Cristaldo *et al.*, 2012).

152 Active nests of this species can harbour many organisms, including other  
153 termite species and invertebrate “termitophiles”, mainly Coleoptera: Staphylin-  
154 idae. Among these latter, *C. melantho* is the most frequent obligatory cohabi-  
155 tant, being present in 80 ~ 83% of the termitaria built by *C. cyphergaster* in a  
156 given region (Cunha & Brandão, 2000; Cristaldo *et al.*, 2012) as long as these  
157 nests are larger than 2.2 litres (Cristaldo *et al.*, 2012).

158 *Corotoca melantho* populations may attain the proportion one beetle per  
159 500 termite workers in a given *C. cyphergaster* nest (Cunha *et al.*, 2015). Un-  
160 der natural conditions, *C. melantho* individuals are reported to live in close  
161 and non-aggressive contact with their termite host (Cunha *et al.*, 2015), engag-  
162 ing interspecific mouth-to-mouth contacts suggestive of trophallactic exchanges  
163 (Seevers, 1957; Rosa *et al.*, 2018). Such contacts are supposed to be facilitated  
164 by the abdominal hypertrophy (“physogastry”) typical of Corotocini, present  
165 in other termitophilous groups, and absent in non-termitophilous Aleocharinae  
166 (Seevers, 1957). By recurving their physogastric abdomen over their thorax,  
167 males and females of *C. melantho* become strikingly similar to termite workers

168 not only in shape but also in size, scaling roughly 1:1 (beetle: termite worker)  
169 (Fig. 1 in Cunha *et al.*, 2015).

170 Physogastry in *C. melantho* females can be attributable to their viviparity  
171 (Reichensperger, 1936) whereas in males it seems derived from an enlargement of  
172 testes (this work). Such abdominal hypertrophy makes *C. melantho* individuals  
173 as mobile as their termite hosts and much less mobile than their confamilial  
174 termitophile beetles bearing a limuloid (horseshoe-crab-shape) body plan. This  
175 impact on mobility can also be partially credited on the vestigialisation of their  
176 posterior wings, which are reduced to a feeble membrane nearly void of venation  
177 (pers. obs.).

178 Trophallactic exchanges are also assumed to be facilitated by the unusual  
179 union observed between the mentum and submentum of Corotocini, which forms  
180 a shield-like sclerite apparently adapted to a liquid diet (Seevers, 1957; Kanao  
181 *et al.*, 2016). This modification is quite rare among other termitophile Aleo-  
182 ocharinae and is absent in all myrmecophile Alleocharinae.

183 As with some limuloid termitophile Aleocharinae (Howard *et al.*, 1980),  
184 physogastric *C. melantho* individuals share cuticular hydrocarbons with their  
185 host but, differently from these limuloid forms, such a chemical similarity seems  
186 acquired rather than innate (Rosa *et al.*, 2018). This trait also seems rele-  
187 vant to the integration of these beetles to the termite society. Interestingly, this  
188 chemical similarity does not prevent *C. melantho* individuals from locating their  
189 sexual mates even in the presence of their termite hosts (Castiblanco-Quiroga  
190 *et al.*, 2017). Also, as with other Aleocharinae (Howard, 1980), *C. melantho*  
191 individuals can follow the scent trail of their host (Castiblanco-Quiroga *et al.*,  
192 2017).

193 One of the least known aspects of *C. melantho* biology is its reproductive  
194 behaviour. Records from as early as 1936 by Reichensperger, *op.cit.*, inform that

195 *C. melantho* females give viviparous birth to well-formed larvae which, according  
196 to Seevers (1957), are ready to pupate. Despite that, no pupa of this species  
197 was ever recorded within a termite nest. A recent finding by Oliveira *et al.*  
198 (2018) seems to shed some light on this issue: *C. melantho* females have been  
199 spotted depositing a larva on the head of a *C. cyphergaster* termite worker in  
200 an outbound foraging trail at night. This could indicate that this termitophiles  
201 pupate outside termitaria, gaining access to termitaria only after emergence by  
202 following their inbound scent trail laid by their hosts. It is plausible to suspect  
203 that, in doing so, these larvae would prevent attacks from termites in this sessile  
204 phasis, when beetles are not morphologically or chemically similar to their host.

205 In spite of the disproportionate number of examples of termitophilic species  
206 among Staphylinidae: Aleocharinae, the evolution of this type of symbiosis in  
207 these beetles remains elusive (Kanao *et al.*, 2016; Yamamoto *et al.*, 2016; Cai  
208 *et al.*, 2017; Yamamoto *et al.*, 2017). Within Aleocharinae, the tribe Corotocini  
209 stands as the largest and most specialized tribe, originated in the Neotropics  
210 in close association with Termitidae: Nasutitermitinae termites (Seevers, 1957;  
211 Jacobson, 1985). Corotocini and its sister tribe Termitonannini belong to a  
212 monophyletic group, and the presence of both tribes in nests of Nasutitermiti-  
213 nae indicates that these tribes evolved from a stock which was already associated  
214 with these termites. Among Corotocini, the most specialised subtribe is Coro-  
215 tocina, in which the genus *Corotoca* is inserted forming a group with the genus  
216 *Spirachtha*. Being present in all Corotocini, physogastry presents the highest  
217 developed forms in the “Corotoca” group (Jacobson, 1985).

218 Limuloid and physogastric body plans are the principal pre-adaptive eco-  
219 morphs allowing termitophily in Aleocharinae beetles (Cai *et al.*, 2017). It seems  
220 non-contentious that the earliest “higher” group Aleocharinae beetles (which in-  
221 cludes Corotocini) are from the Paleogene: Eocene, *c.a.* 45 mya, whereas the

222 earliest Termitidae termites (in which Nasutitermitinae: *Constrictotermes* are  
223 included), are from the transition between the Paleogene: Paleocene to the Pa-  
224 leogene: Eocene, *c.a.* 55 mya (Engel *et al.*, 2009; Cai *et al.*, 2017). Despite  
225 ongoing discussion on the actual timing for the onset of termitophily in the  
226 evolutionary history of Aleocharinae (Yamamoto *et al.*, 2017), authors tend to  
227 agree that (i) limuloid and physogastric morphs evolved independently; (ii) the  
228 limuloid morph appeared earlier, as an adaptation to living under tree barks and  
229 in leaf litter, being posteriorly co-opted for defence; and (iii) while limuloids are  
230 adapted to hide and avoid contacts with their hosts, physogastrics engage in  
231 frequent guest-host interactions (Kanao *et al.*, 2016; Yamamoto *et al.*, 2016;  
232 Cai *et al.*, 2017).

## 233 **2.4 Study area and sampling**

234 Undamaged arboreal nests of *C. cyphergaster* were collected in Brazilian sa-  
235 vanna (“Cerrado”), near the town of Sete Lagoas (19°25’02.3” S, 44°09’30.2”  
236 W and 19°25’04.2” S, 44°09’30.5” W) in October 2014 and near Divinópolis  
237 (20°10’28.5” S, 44°49’32.3” W) in July 2015. Both locations are within the state  
238 of Minas Gerais, South-eastern Brazil. The altitude of the study site varies from  
239 700 to 900 m above sea level, in a region subjected to Köppen’s equatorial with  
240 dry winter (Aw) climate. In the laboratory, nests were completely dissected and  
241 inspected to collect termitophilous Staphylinidae. Specimens were preserved in  
242 80% alcohol. Specimens were identified to species by comparison with samples  
243 from the Termite Section of the Entomological Museum of the Federal Univer-  
244 sity of Viçosa (MEUV), where vouchers were deposited.

## 245 **2.5 Morphology**

246 Beetles of both sexes have been removed from their housing termite nests and  
247 transferred to in 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer, pH  
248 7.2, containing 3% sucrose and 0.2% picric acid for 48h at 5°C. Then, abdomens  
249 were detached from the beetles' body, dehydrated in a graded ethanol series (70,  
250 80, 90 and 95%) and embedded in hystoresin JB-4. Semi-thin sections (3  $\mu$ m  
251 thick) were obtained using a microtome (Leica™ RM2255) with a glass knife,  
252 stained with Harris hematoxylin and eosin, and analysed and photographed in a  
253 light microscope (Olympus™ BX-60 with camera Q Color 3). Other individuals  
254 were cryoanesthetized (-4°C) and dissected in 0.1 M sodium phosphate buffer,  
255 pH 7.2 to extract and photograph the whole reproductive tract. Reproductive  
256 organs were then analysed and photographed using a Zeiss™ Discovery V-20  
257 stereo-microscope with an AxioCam MRc camera.

## 258 **3 Results**

259 A total of 14 adult *C. melantho* beetles have been inspected (eight females and  
260 six males). Physogastry in females was more pronounced than in males (Fig. 1).  
261 Wing venation is vestigial.

262 Females present two meroistic telotrophic ovaries connected to the lateral  
263 oviducts which end on the common oviduct and thence to the vagina (Fig. 2  
264 B, 3 A). Each ovary has a pair of tubular ovarioles, short, pale coloured or  
265 yellowish, connected at the distal part by the terminal filament (Fig. 2 B, 3  
266 A). The ovariole is coated by a thin peritoneal sheath formed by flattened cells,  
267 extending parallel to the non-cellular basal lamina until the terminal filament  
268 (Fig. 3 B). The tropharium is short and formed by trophocytes of uniform  
269 size (Fig. 3 B). The vitellarium is well expanded bearing, in its distal part,

270 some previtellogenic oocytes and a large vitellogenic oocyte in the proximal  
271 part surrounded by the follicular cells (Fig. 3 B).

272 The ovarioles show an asynchronous development of the oocytes: while an  
273 ovariole shows a well developed vitellogenic oocyte, the other ovarioles present  
274 oocytes in early developmental stages (Fig. 2 B, 3 A). The pedicel is minimal;  
275 the lateral oviduct is short and connected to the common oviduct (Fig. 3 A).  
276 The common oviduct is expanded to simultaneously house a set of embryos and  
277 larvae according to the reproductive stage of the female (Fig. 2 A, B).

278 Quite frequently in each of the eight dissected females, a developing em-  
279 bryo surrounded by copious amounts of yolk was found in the common oviduct  
280 (Fig. 2 B, C) along with larvae forming a gradient of growth stages (Fig. 2 A,  
281 B, D, E). A maximum of one embryo plus two larvae bearing distinct body  
282 segments, ocelli, mouthparts, legs and body setae (Fig. 2 A, B, D, E ) could  
283 be observed simultaneously in the common oviduct of a single female. No sper-  
284 matheca was detected in females.

285 In males, each testis is formed by four follicles disposed in parallel and con-  
286 nected separately by the efferent duct to a short and narrow deferent duct whose  
287 diameter is constant along its full length. Follicles are enlarged: testes occupy  
288 about 80% of the abdomen of the male, being hence mostly responsible for  
289 physogastry in these individuals. All stages of spermatogenesis have been found  
290 in the testes (spermatogonia, spermatocytes, spermatids, spermatozoa, Fig. 4).  
291 Spermatogenesis begins at a short germarium on the distal part of the testis fol-  
292 licle which ends in a primary growth zone where the spermatogonia (Fig. 4 A)  
293 and spermatocytes (Fig. 4 B and C) are found. The development of these cells  
294 continues until the spermatids (Fig. 4 D and E) become filiform spermatozoa  
295 organised in bundles (Fig. 4 F). A pair of accessory glands, forming a loop at  
296 their mid part, opens at the anterior part of the ejaculatory duct. The ejacu-

297 latory duct comprises a subtly narrowed anterior section, where deferent duct  
298 and accessory glands open, followed by a wider midsection tapering towards the  
299 posterior section, which is connected to the genitalia.

## 300 4 Discussion

301 Integration of termitophile staphylinids in their termite host colony is indis-  
302 putable as they often –being physogastric or not– engage in intimate tactile  
303 contacts with their hosts (Howard, 1980; Kistner, 1982). Here we present an  
304 additional facet of this integration (Fig. 5): physogastric *C. melantho* beetles  
305 seem to show alignment between their reproductive traits and their housing  
306 termitarium, suggesting convergence with troglobitic species and cave habitats  
307 (Poulson & White, 1969).

308 Whether or not such an alignment has evolved as a cause or a consequence of  
309 termitophily is still uncertain. It could have arisen because (i) the beetle sought  
310 shelter in termitaria and hence suffered pressure to integrate into the termite  
311 colony, or (ii) frequent interactions between foraging termites and beetle in-  
312 dividuals forged an interspecific link which resulted in the beetle establishing  
313 itself in termitaria. We hope to shed some light on such a conundrum through  
314 a first approximation of the proximate and ultimate causes of this behaviour  
315 under the framework proposed by Tinbergen (1963) and reviewed recently by  
316 Bateson & Laland (2013). To do so, we ask “what is the purpose of termitophily  
317 in *C. melantho*?” inspecting some mechanistic and ontogenetic causes (proxi-  
318 mate) and hinting on the adaptive value and the evolutionary history (ultimate)  
319 underlying this behaviour.

## 320 4.1 Mechanism

321 A series of morpho-physiological and behavioural traits seem to contribute to  
322 elicit termitophily in *C. melantho*. Viviparity and its consequent physogastry  
323 (Figs. 1 and 2) would imply prolonged periods of vulnerability for pregnant  
324 *C. melantho* females, while testes enlargement leading to physogastry in males  
325 could have similar effects. Physogastry and wing vestigialization should also  
326 impair mobility, so that both, females and males, could conceivably favour a  
327 sedentary life in a sheltered and enclosed environment such as termitaria.

328 The asynchronous development of the oocytes resulting, at any given time,  
329 in just one vitellogenic oocyte amongst less developed others (Fig. 2) points  
330 not only to long-term pregnancy but also to recurrent matings, and that seems  
331 reinforced by the detection of a full developing sequence of sperm cells in the  
332 testes of the male indicating continuous spermatogenesis in this species (Fig. 4).  
333 Again, an enclosed habitat might allow recurrent matings by enhancing inter-  
334 individual contacts. This appears further evidenced by the presence of several  
335 male beetles as well as both, fertilised and non-fertilised females, as also noticed  
336 by Seevers (1957) and Schiødte (1853) in termitaria of this same host species.

337 Once inside a termitarium, beetles can acquire cuticular hydrocarbons from  
338 their hosts (Rosa *et al.*, 2018) which, combined with their physogastric resem-  
339 blance to termite workers, might ease allogrooming leading to social integration.  
340 The fused mouthparts adapted to liquid feeding in these beetles (Seevers, 1957)  
341 seem to indicate that the mouth-to-mouth contacts frequently observed between  
342 them and their host could in fact involve trophallactic exchanges.

343 The hypothesis that these beetles are adapted not only to the termite colony  
344 but also to its physical structure finds further support on the reduction of ovar-  
345 ioles in females of *C. melantho* as compared to other members of its subfamily  
346 (Aleocharinae). While in these latter around six ovarioles are common (Welch,

347 1993), in *C. melantho* we have found only two in each ovary (Fig. 3). Interest-  
348 ingly, both viviparous (Hagan, 1951) as well as subterranean and troglobiont in-  
349 sects (Faille & Pluot-Sigwalt, 2015) also present a similar reduction in ovarioles,  
350 laying fewer but larger eggs than con-familiar ones. Additionally, troglobiont  
351 organisms tend to present diminished reproductive rates and increased invest-  
352 ment in the offspring, such features seeming plausibly inferred from the number  
353 of ovarioles and the viviparity here observed in *C. melantho*.

## 354 4.2 Ontogeny

355 Developmental changes across the lifespan of termite colonies and beetles also  
356 seem relevant to explain this termitophilic relationship. There appears to be  
357 a threshold in nest size (volume  $\geq 2.2$  L) above which *C. cyphergaster* host  
358 colonies are more prone to invasion by staphylinids (Cristaldo *et al.*, 2012). It  
359 is however still uncertain whether this threshold is related to the termite colony  
360 ontogeny or to the physical development of the nest itself.

361 As for the ontogeny of the termitophile, it is already known that full grown  
362 reproductive adults are frequently found within termitaria whereas no beetle  
363 larvae or pupae have been ever found within such nests. However, a recent  
364 report by Oliveira *et al.* (2018) on *C. melantho* females depositing a larva on the  
365 head of a termite in a foraging party seems to indicate that these termitophiles  
366 pupate outside their host termitaria. In order to resume a termitophilic life,  
367 newly emerged adults of *C. melantho* would merely use their scent following  
368 ability (Castiblanco-Quiroga *et al.*, 2017) to locate a termitarium via its inbound  
369 foraging trails. This would be possible because foraging trails built by these  
370 termites are well marked in the open and are often reutilised (Moura *et al.*,  
371 2006). This hypothetical reproductive strategy seems in line with the fact that  
372 such beetles never attain large populations within termitaria, being found at a

373 rate of 1 beetle to 500 termite workers (Cunha *et al.*, 2015). That is, by leaving  
374 the nest to pupate outside, larvae may impose a time lag in an otherwise fast  
375 build-up of the *C. melantho* population.

376 In short, termitophily by *C. melantho* seems to depend on the correct adjust  
377 between the development of the termite nest, the beetle reproductive strategy  
378 itself, and the development of the beetle populations. Whether these adjust-  
379 ments are connected with the carrying capacity of the termite colony or of the  
380 termite nest is still open to investigation.

### 381 **4.3 Adaptive value**

382 Host-guest direct interactions such as allogrooming and trophallaxis are advan-  
383 tageous for the survival of *C. melantho* individuals, as these behaviours provide  
384 hygienic and feeding care. Similarly, beetles' resemblance to termite workers (via  
385 physogastry, as well as chemical or walking similarity) could favour survival if  
386 this trait would serve as a disguise against non-termitophagous predators spe-  
387 cialised on termitophiles. In this way, a palatable beetle's resemblance to an  
388 unpalatable termite would protect the former against visually- or scent-oriented  
389 predators, in a typical Batesian mimicry. de Visser *et al.* (2008) have already  
390 reported the presence of such predators within termite nests, whereas Oliveira  
391 & Sazima (1984) and Uma *et al.* (2013) have demonstrated the protective gains  
392 from Batesian mimicry, at least for myrmecomorphic spiders.

393 In addition to the organismic level, a further adaptive value of termitophily  
394 seems to reside at the termitarium level: the troglobitic-like traits of *C. melan-*  
395 *tho* might impel these beetles to seek for termitaria as shelter. Despite being  
396 proposed here for the first time as a complementary driver of termitophily, this  
397 is not at all a novel hypothesis in the study of termite macro-symbioses. Nearly  
398 50 years ago, Araujo (1970) has speculated that some organisms would seek

399 termitaria for shelter (but, differently from us, he has not enlisted any trait  
400 potentially connected to it). He termed these organisms “termitariophiles”,  
401 from the Latin-rooted “termitarium” (termite nest) and the Greek “phylos”  
402 (friend). More recently this dependence by invaders on the physical structure of  
403 the termite nest has been demonstrated at the community level, again without  
404 any mention to individual traits (Marins *et al.*, 2016; Monteiro *et al.*, 2017).  
405 This would lend confidence to the notion that shelter provided by a termitar-  
406 ium could indeed promote the survival of vulnerable physogastric individuals.  
407 Likewise, the enclosure provided by termitaria walls would favour continuous  
408 reproduction of frequently mating individuals.

409 In summary, it seems plausible to consider that the adaptive value of ter-  
410 mitophily for such beetles may derive from selection directed at the organismic  
411 and at the physical level, that is, the termite individuals and the termite nest,  
412 respectively.

#### 413 4.4 Phylogeny

414 The evolutionary explanations describing the history of termitophily in Coro-  
415 tocini in general, and in *C. melantho* in particular, seem intricately tied to four  
416 traits presented by this tribal branch in Staphylinidae: physogastry, mentum  
417 fused to submentum, free mesocoxae, and chemoreceptory sensilla on the termi-  
418 nal antennomeres (Seevers, 1957). Together, these traits seem to provide useful  
419 adaptations for an interactive life within a termitarium because while physogas-  
420 try could facilitate interspecific tactile contacts, fused mouthparts would allow  
421 trophallaxis, leg adaptations would attenuate mobility impairments imposed by  
422 physogastry, and chemoreceptory sensilla should enable inter- and intra-specific  
423 scent recognition. Monophyly in this tribe (Seevers, 1957; Jacobson, 1985) seems  
424 to support the hypothesis that the common ancestral to all Corotocini was well

425 equipped for termitophily.

426       However, since termitophiles are also found among other branches of Aleocharinae lacking a full set of these traits, one cannot consider them as an  
427       exclusive pre-condition to termitophily. Moreover, Corotocini, being part of the  
428       “higher” Aleocharinae, would have a limuloid stock among their early ancestrals  
429       (Yamamoto *et al.*, 2016; Cai *et al.*, 2017). The limuloid body shape, in its turn,  
430       seems to be an adaptation do living under tree barks and in leaf litter, being  
431       posteriorly co-opted for defence in a termitophilic context (Kanao *et al.*, 2016).  
432       Therefore, the propensity to live in dark and enclosed spaces seem ancient in  
433       Aleocharinae.  
434

435       It seems plausible, then, to consider that *C. melantho* would have inherited  
436       from its ancestrals both, the morpho-physiological interactive apparatuses and  
437       the propensity to live in dark places.

#### 438   **4.5 Conclusion**

439       Being a consequence of viviparity (in females) and testes enlargement (in males),  
440       physogastry in *C. melantho* – as suggested by Kistner (1982, p.2) regarding  
441       Staphylinidae in general – seems not ascribable to the action of natural selec-  
442       tion directed solely at the termite individuals themselves. As evidenced by our  
443       results, its links to termitophily seem more conservatively interpreted as a com-  
444       bination of factors including not only termite-beetle inter-individual interactions  
445       but also the demands of the beetle for the environment provided by the physi-  
446       cal structure of the termite nest. This hypothetical integration between causes  
447       for termitophily is summarized in Fig. 5. We warn, however, that even though  
448       plausible and supported by the evidence provided here, this should still be taken  
449       as a hypothesis. A throughout re-examination of such traits in other systems of  
450       social parasites or inquilines might reveal unforeseen research avenues not only

451 on termitophily or myrmecophily but on mechanisms underlying symbioses in  
452 general.

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## 478 **Contribution of authors**

479 ODS conceived the hypothesis. RMP collected the insects. RMP, KS, and JES  
480 planned the morphological observations. RMP and KS conducted the morpho-  
481 logical data collection. RMP, KS, and JES conducted morphological analyses.  
482 JLN, RMP, and KS carried out photographic documentation. ODS and RMP  
483 wrote the text. ODS and JES arranged funding. All authors reviewed the  
484 manuscript.

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615

616 **Figure legends**

Figure 1: Lateral view of male (A) and female (B) individuals of *Corotoca melantho*. Scale: 500  $\mu\text{m}$

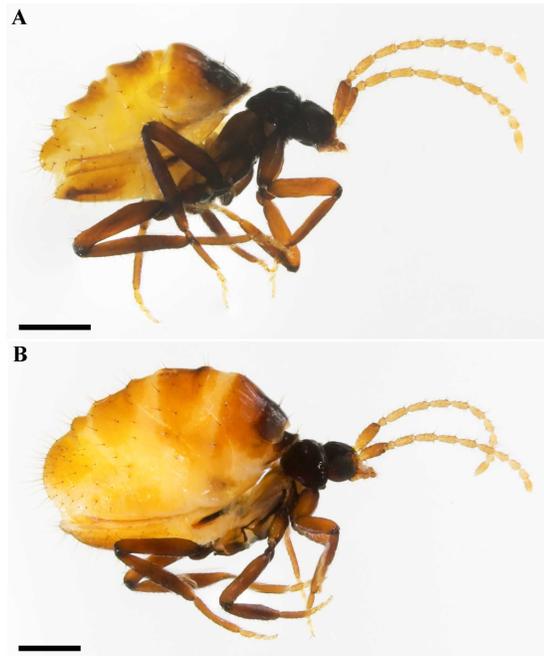
Figure 2: Female's reproductive tract of *Corotoca melantho* (Coleoptera: Staphylinidae): (A) spatial organisation of embryos and larvae in the abdomen of a pregnant female. The arrow indicates the direction of developed of the offspring (ovaries are not show); (B) overall depiction of the reproductive tract of a female. Note in the common oviduct one embryo and one larvae; (C) embryo surrounded by yellow yolk; (D, E) developing larvae. **as** abdominal segment; **co** common oviduct; **lo** lateral oviduct; **o** ovary; **vg** vagina. Scales: (A) 50  $\mu\text{m}$ ; (B) 40  $\mu\text{m}$ ; (C-E) 20  $\mu\text{m}$

Figure 3: Ovary of *Corotoca melantho* (Coleoptera: Staphylinidae): (A) the ovaries have two ovarioles, and in each one the oocytes present asynchronous development; (B) longitudinal histological section of one ovariole. **fe** follicular epithelium; **lo** lateral oviduct; **oo** oocyte; **ov** ovariole; **tf** terminal filament; **ps** peritoneal sheath; **tr** tropharium; **vg** vagina; **vt** vitellarium. Scales: (A) 20  $\mu\text{m}$ ; (B) 30  $\mu\text{m}$ .

Figure 4: Spermatogenesis in *Corotoca melantho* (Coleoptera: Staphylinidae): (A) longitudinal histological section of one testicular follicle showing cyst in different stages of spermatogenesis (some cysts are indicated with dotted lines); (B, C) cysts with spermatocytes; (D, E) cyst with spermatids in successive stages of development; (F) sperm bundles (arrows). **cy** cyst; **f** flagellum; **gm** germarium's zone; **n** nucleus. Scales: (A) 30  $\mu\text{m}$ , (B-F) 10  $\mu\text{m}$

Figure 5: Diagramatic concatenation of some evidence leading to the hypothesis that the integration of *Corotoca melantho* (Coleoptera: Staphylinidae) in termite colonies is based simultaneously on interactions between this termitophile and its host termites (*i.e.*, termitophily) and between such an invader and its host termitarium (*i.e.*, termitariophily). Even though the routes here depicted are not established facts yet, they would serve to illustrate how a single trait, such as physogastry or wing vestigialization, might simultaneously underlie the routes to termitophily and termitariophily.

Figure 1



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Figure 2

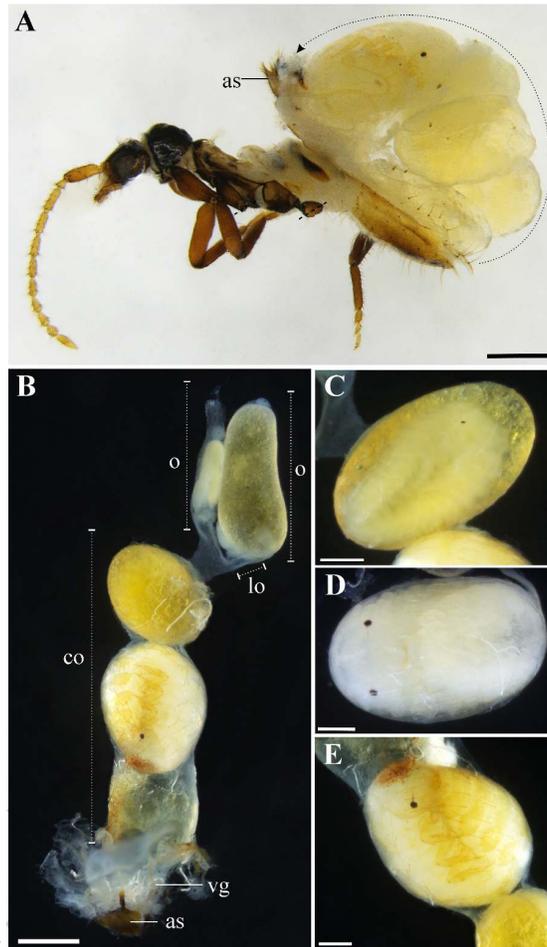
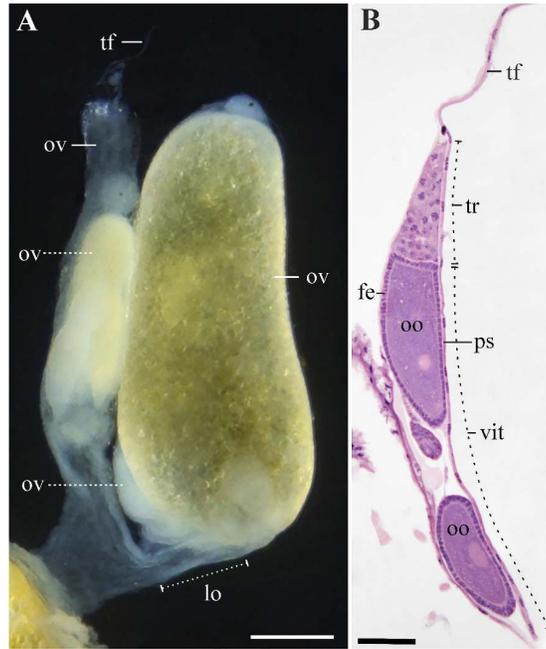


Figure 3



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Figure 4

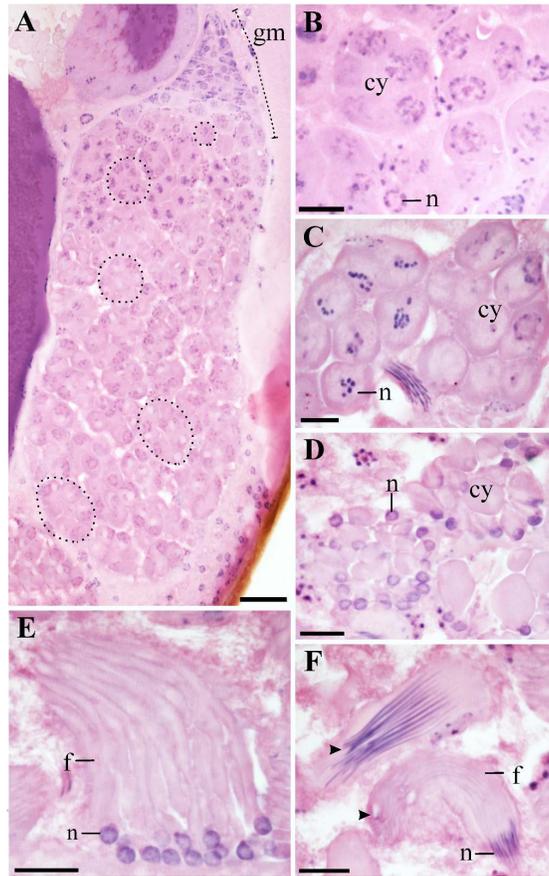
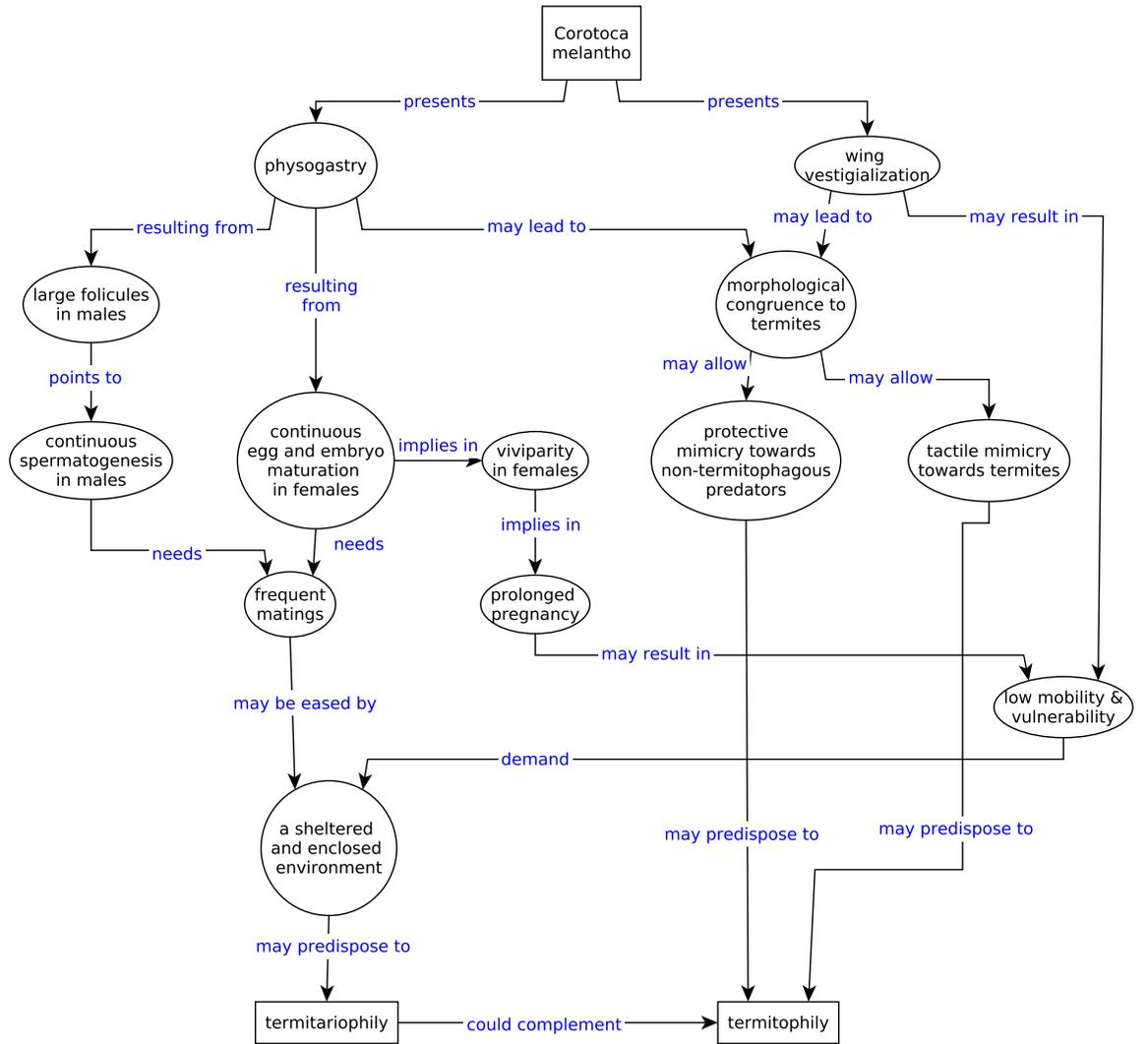
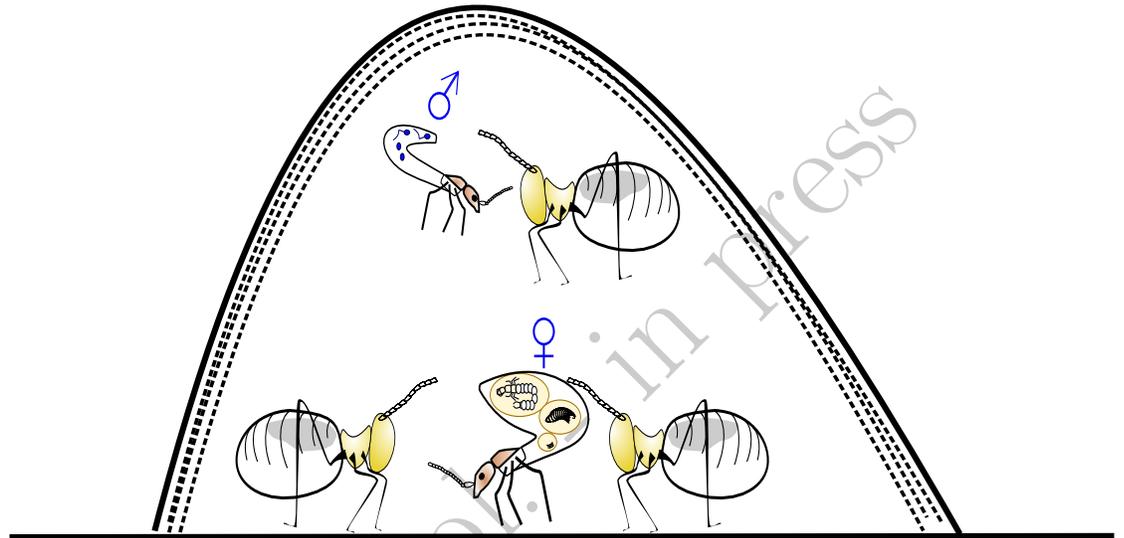


Figure 5



Graphical abstract



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