

State of knowledge of viviparity in Staphylinidae and the evolutionary significance of this phenomenon in *Corotoca* Schiødte, 1853

Bruno Zilberman¹; Carlos Moreno Pires-Silva^{2,4}; Igor Eloi Moreira^{2,5}; Raul Marques Pisco³; Maria Avany Bezerra-Gusmão^{2,6}

¹ Universidade de São Paulo (USP), Museu de Zoologia (MZUSP). São Paulo, SP, Brasil.

ORCID: <http://orcid.org/0000-0003-2613-4827>. E-mail: brunozilberman@usp.br

² Universidade Estadual da Paraíba (UEPB), Departamento de Biologia (DEPBIO), Laboratório de Ecologia de Térmitas. Campina Grande, PB, Brasil.

³ Universidade Norte do Paraná (UNOPAR), Departamento de Biologia (Polo Teresópolis). Teresópolis, RJ, Brasil.

ORCID: <http://orcid.org/0000-0003-4803-6988>. E-mail: raulpisco@gmail.com

⁴ ORCID: <http://orcid.org/0000-0002-6195-8648>. E-mail: carlospsilvamoreno@gmail.com

⁵ ORCID: <http://orcid.org/0000-0001-8013-8963>. E-mail: eloi.igor@yandex.com

⁶ ORCID: <http://orcid.org/0000-0002-1227-3167>. E-mail: bezerra.gusmao@uepb.edu.br

Abstract. Viviparity is characterized by the retention of fertilized eggs in reproductive tract of the female. This condition is very common in vertebrates, but relatively rare in invertebrates, including insects. The present work presents a review on viviparity in Staphylinidae, with special attention on genus *Corotoca* Schiødte, 1853. The genus is composed by six termitophilous species with neotropical distribution, and together with *Spirachtha* Schiødte, 1853 are the only to genera with species confirmed as viviparous in the family. Also, information and discussion are presented on the life cycle of *Corotoca* species based on dissection of females in laboratory and field observations. During the dissection of females of four species of *Corotoca* we observed that each female carries three eggs at the same time. The embryos present asynchronous development: when one is located at apex of abdomen, the other two are at IV segment, on abdomen curvature. These observations are complementary with those obtained in field observation, when the female deposits a larva outside the nest, on the foraging trail of termite *Constrictotermes cyphergaster* (Silvestri, 1901). The strategy of *Corotoca* species focused on the immature as dispersing agent is derived and probably favor the fitness in relation to a hypothetical condition in which the adult is the dispersive agent.

Key-Words. Termitophily; Neotropical; Rove Beetles; Corotocini.

INTRODUCTION

The viviparity is characterized by the retention of fertilized eggs in reproductive tract of the female. In this case, the development of the embryo rather than occurs on the external environment, occurs inside the female abdomen (Hagan, 1948; Clutton-Brock & Scott, 1991). This phenomenon/condition is broadly distributed in vertebrates, with notable exception of birds (Blackburn & Evans, 1986), and evolved independently in more than 150 lineages. Although the viviparity in insects is proportionally rare, the list is gradually increasing and encompassing diverse taxonomic groups (Hagan, 1951; Meier *et al.*, 1999).

Up to now, the main works on viviparous insects are Hagan (1948, 1951). Related to Coleoptera, he compiled the cases of viviparity for Micromalthidae, Staphylinidae and Chrysomelidae. For the next 50 years, the new registers for this phenomenon are related to three

tribes of Tenebrionidae (Oncotini, Platynotini and Ulomini) (Tschinkel, 1978; Iwan, 2000; Dutrillaux *et al.*, 2010), one genus of Carabidae (*Pseudomorpha* Kirby (Liebherr & Kavanaugh, 1985)), and one genus of Cerambycidae (*Borneostyrax* Gabriš (Gabriš *et al.*, 2016)). Glaçon-Deleurance (1963) stated that beetles from tribe Leptodirini (Leiodidae), extremely modified for cavernicolous habitus, apparently deposit a single egg already with a fully developed larva.

After an overview on the state of knowledge on viviparous condition in staphylinid beetles, it is presented a detailed study of this condition for the genus *Corotoca* Schiødte, 1853 with information obtained from field and laboratory observations. It is also placed a discussion on the possible evolutionary and ecological meaning of this reproductive adaption in the context of termitophily. This work represents an important contribution to the reproductive behavior of termitophilous beetles, including new data to the scarce knowledge.

Pap. Avulsos Zool., 2019; v.59: e20195919

<http://doi.org/10.11606/1807-0205/2019.59.19>

<http://www.revistas.usp.br/paz>

<http://www.scielo.br/paz>

Edited by: Simone Policena Rosa

Received: 12/11/2018

Accepted: 26/02/2019

Published: 03/04/2019

ISSN On-Line: 1807-0205

ISSN Printed: 0031-1049

ISNI: 0000-0004-0384-1825



Terminology: Viviparity, Ovoviviparity and Larviparity

Hagan (1948) strictly defined viviparity in insects as the process in which they “give birth to living offspring which have hatched from the egg within the mother’s body”. The author however recognized the fact that some species can deposit eggs with embryos in different stages of development, and considered this behavior as a different phenomenon, called “ovoviviparity”. Later, Hagan (1951) presented a new classification, where the viviparity of insects is classified in four groups, based on the modifications related to the strategies utilized to nourish the embryo during the development:

Ovoviviparity – the egg contains enough yolk to nourish the embryo till hatching. No special structures are associated with the embryo nourishment.

Adenotrophic viviparity – the egg contains enough yolk to nourish the embryo till hatching. Special structures are associated with the embryo nourishment.

Haemocoelous viviparity – the development of the embryo occurs in the haemocoel, not in genital ducts. Embryonic nourishment is derived from maternal tissue.

Pseudoplacental viviparity – the embryo obtains at least part of nourishment by means of a pseudoplacenta.

The disponible terminologies adopted to classify the viviparity are several times confuse and variable depending on the author. Sellier (1955) suggests that any species that incubate the egg, even for a short period of time, should be classified as ovoviviparous. However, Weber (1933) previously considered ovoviviparity when the eggs hatch larvae during or immediately after oviposition. Weber as well followed the strict definition of viviparity by Hagan (1948), towards only for species whose larva, not the egg in any circumstance is deposited.

The attempt to classify certain species of viviparous insects may be unsuccessful as Bontems (1984) shows in his paper on viviparity of Chrysomelidae. The author stated that for certain groups, the Hagan’s (1951) classification is dispensable because they may present numerous intermediate cases. According to this author, during the reproductive period, even in a same species, it is possible to observe the deposition of eggs with embryos in different stages of development, or even the larva completely developed, after hatching the egg inside the female abdomen. Based on these observations, the author chose the Carayon’s (1962) classification, which considers that viviparous is any species that at least part of embryo’s development occurs inside the progenitor (which agrees with our general concept of viviparity).

The difficulty to classify things that compose a fraction of a gradient is what Dawkins (2011) called “the tyranny of discontinuous mind” and indeed, this difficulty can generate pseudoproblems associated with fruitless discussions, taking away from the focus of real problem. The difficulty in differentiating larviparity (the extreme of the spectrum of viviparity) from oviparity is due the

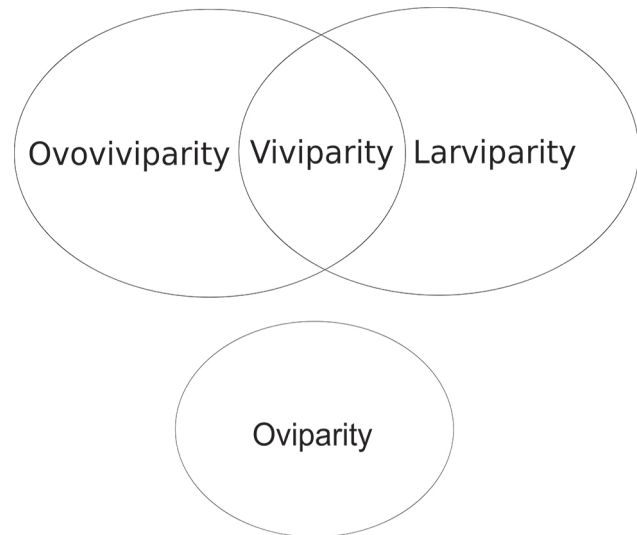


Figure 1. Classification model for viviparous beetles.

lacking or loss of the intermediate stages between the two extremities of the spectrum through evolutionary history. Therefore, for species that hold a continuous strategy of viviparity, perhaps it is important to ask questions about the evolutionary and ecological implications of maintaining this gradient rather than trying to categorize something that maybe is not categorizable.

In this work the viviparity and oviparity are defined as following, i) Oviparity – egg deposition with the embryo’s fully development occurring outside of parental body, ii) Viviparity – the deposition of eggs already incubated within the parental organism (no matter the stage of embryo’s development) or deposition of larva fully developed, after egg hatching.

Based on this definition, it is possible to subdivide the viviparity in two categories, a) Ovoviviparity: the viviparity in which the larva exits the egg immediately or later, following oviposition; b) Larviparity: the viviparity in which the larva is deposited completely developed or hatching the egg during the oviposition. This subdivision implies that a viviparous organism could be additionally classified as larviparous or ovoviviparous. This specificity in classification only can occur in the light of evidences. It is not possible to classify a species as ovoviviparous without checking if an egg already incubated by the female is deposited, instead of a free larva. On the other hand, larviparous condition could be inferred if it is found larvae fully developed in abdomen, without an egg shell (Fig. 1).

Viviparity in Staphylinidae

Staphylinidae is one of the largest families in Coleoptera, comprising about 62.820 species (Newton, 2017), and the viviparous condition in the group is rare, recorded only for species of two termitophilous genera of tribe Corotocini Fenyes, 1918 – *Corotoca* Schiødte, 1853 and *Spirachtha* Schiødte, 1853. For this tribe, Warren (1920) hypothesized that the species of *Paracorotoca*

Warren, 1920, are viviparous, but this was not confirmed. It was also supposed that *Lomechusoides strumosus* (Fabricius, 1775) and *Lomechusa pubicollis* (Briscout de Barneville, 1860) (two myrmecophilous species of Lomechusini Fleming, 1821), present cases of viviparity, still not confirmed (Jordan, 1913; Wasmann 1915a, b; Donisthorpe, 1917, 1926).

Since *Lomechusoides* eggs were two times misidentified as ant eggs, and the deposition of eggs in *L. pubicollis* was never found, Wasmann (1915a, b) was convinced that the species of this genus are viviparous. He argued that the observations were taken for thirty years, but the problem with his conclusion is that his argument can be considered as the well-known problem that “absence of evidence is not evidence of absence”. The fact that he couldn’t observe evidence of oviparity – for example, a laying of an egg – does not mean that the species are viviparous. In other words, as Hagan (1948) pointed out, his evidence “is pure circumstantial” since he did not see neither oviposition nor larviposition, and it is unknown how larvae appeared in formicarium.

Hagan (1951) cited Donisthorpe and Jordan on the debate about the viviparity of these species. Contrary to what Iwan (2000) claimed, Donisthorpe (1917, 1926) did not question Wasmann’s affirmation on viviparity of this species and accepted his deductions. Donisthorpe claims, referring to Wasmann (1915a, b), that “this beetle – *Lomechusoides strumosus* – is viviparous, tiny live larvae being deposited by parent beetle on to the brood of the host”. Donisthorpe (1917), however, seemed to have had the chance to close the matter from his observations, as the author lamented: “(...) I missed the important part, or did not wait long enough to complete the observation”. Later on, Hölldobler *et al.* (2018) stated that their histological work did not “indicate any sign of ovoviviparity”.

The tribe Corotocini encompasses termitophilous physogastric beetles associated mostly with termites of subfamily Nasutitermitinae. It is composed by about 200 species, separated in 61 genera (first author’s personal database). Schiødte (1853) presented the first record of insects living within termite nests and the three species he described (*Corotoca melantho*, *C. phylo* and *Spirachtha eurymedusa*), even today with more than 200 species in the tribe, constitute a group encompassing one of the most modified termitophilous beetles known to science. Besides that, those species were the first cases of supposed known viviparity in Staphylinidae.

Due to the impressive morphological adaptations and physogastry on those termitophilous aleocharinae, Schiødte called them “stranger guests” in which the abdomen is “constructed in a most extraordinary manner”. Even inside the subfamily Aleocharinae, with more than 15 thousand species, the termitophily probably evolved more than 10 times (Kistner, 1969). Otherwise, the viviparous condition in whole Staphylinidae family, with more than 60 thousand species, was supposed to occur only in the two genera that Schiødte established that time.

Schiødte (1853, 1856) observed in the female abdomen eggs with embryos in various stages of develop-

ment in both genera and even eggs with fully developed larvae in *Corotoca*. It is not clear, however, whether he observed in the two species of *Corotoca* or only one. The search led Schiødte to confirm the viviparity in the three species, although in *Spirachtha eurymedusa* he found only embryos in the early stages of development. After Schiødte’s description of *C. melantho* and *C. phylo*, other four species for the genus have been described so far: one species from Guyana, *C. guyanae* Mann, 1923; two from Brazil, *C. araujo* Seevers, 1957, *C. fontesi* Zilberman, 2018 and one from Brazil and Argentina, *C. pseudomelantho* Zilberman, 2018 (in Zilberman & Casari, 2018). Although none of these papers added knowledge about the viviparous condition of the genus, the phenomenon was often verified throughout history, including by the authors of this paper.

In contrast, there is no other case of verification of viviparity in *Spirachtha*, apart from Schiødte’s partial observation in 1853. We dissected females of *S. eurymedusa* and no evidence was found suggesting it is viviparous. Which is strange, since dissecting any female of the *Corotoca* species, from any locality and period will eventually result in material that shows the presence of the condition in the species. Because of that, it is possibly reasonable to claim that Schiødte could be biased and the viviparity in *Spirachtha* is yet to be confirmed.

In his classic and important work on viviparous insects Hagan (1951) also had little to say about the viviparity in the staphylinid genera, and only recently this stagnation of more than one and a half century begun to change. Oliveira *et al.* (2018) observed that *Corotoca* species deposit the larva outside the nest, in the foraging trail of *Constrictotermes cyphergaster*.

For the other genera of the tribe Corotocini, there is not any hypothesis on viviparous occurrence except for the genus *Paracorotoca* Warren, 1920. The author considered the genus as probably viviparous based on studies on *P. akermani* (Warren, 1914), from South Africa. Since then, three South-west African species have been described so far: *P. coatoni* Kistner, 1970, *P. quadrilobatus* Kistner, 1970 and *P. sheasbyi* Kistner, 1970, and no mention was made about viviparity condition for those species (Kistner, 1970). Warren suggested the possibility of viviparous condition in the genus *Paracorotoca* based on the morphological similarity with *Corotoca*. He found larvae inside the nest, but none inside the female abdomen. No egg nor pupa was found inside or outside the nest. Besides, the well-developed reproductive system in *Paracorotoca*, which is largely responsible for the size of the abdomen, and the reduced number of relatively large eggs filled with veal globules, led Warren to assume the viviparity condition for the genus. According to the author, the large eggs would carry developing larvae. This statement would be corroborated by records in the genus *Corotoca*, which also have a large abdomen and reduced number of eggs, large, filled with veal and at least confirmed for *Corotoca* – each with a developing larva.

A peculiarity of the genus *Paracorotoca*, however, is the proportion of adults in relation to the number of

larvae found in host nests. Warren (1920) reported that when studying nests, there were at least twenty times more larvae than adults. Kistner (1976) found 990 larvae and only five adults, that is, 198 times more larvae than adults. It is a scenario that differs from that found in *Corotoca*, in which no larva was ever found inside the nest, except inside the female abdomen. Therefore, the viviparity of the genus *Paracorotoca* is yet to be confirmed.

After these considerations, this work brings contributions with further observations regarding to the viviparous condition of the genus *Corotoca*, including those from the internal anatomy of dissected females and field observation. It is also presented a discussion about the "ultimate questions" surrounding *Corotoca* species' reproductive behavior.

METHODS

Study Area – Field Observations

The field work was conducted in "Estação Experimental São João do Cariri" located at São João do Cariri municipality (36°31'W; 07°22'S), Paraíba State, northeastern of Brazil (Fig. 2). The Experimental Station is situated in a dry forest biome and have an area of 310 ha with arbustive vegetation predominant (Barbosa *et al.*, 2007). The Cariri is an arid region of Brazil, with altitudes ranging from 400 to 700 m a.s.l. The mean rainfall is 400 mm/year and

variability of 84 and 93 mm/year. Relative humidity is approximately 70% and evapotranspiration is 2,000 mm/year, which characterizes this region by a high annual variability in rainfall precipitation (Araujo, 2005).

The foraging of 20 nests of *C. cyphergaster* were monitored during the whole foraging event. Ten nests were monitored for 20 days in Nov/2017, 5 nests during 6 days in Jan/2018, and other 5 nests during 7 days in Apr/2018. It was observed the female of *Corotoca* following and interacting with termite hosts. A single larva was captured alive but rearing in laboratory was not successful. New attempts are currently under procedure.

Observation in laboratory – Dissections

Females of all species of *Corotoca*, except *C. araujoi*, were observed during dissection to evaluate the evidences of viviparity related to internal anatomy. It was studied seven specimens of *C. melantho*, one of *C. phylo*, three of *C. fontesi*, two of *C. pseudomelantho* and one of *C. guyanae*. All specimens belong to collection of the "Museu de Zoologia da Universidade de São Paulo" (MZSP).

The dissection of the specimens of the *Corotoca* species were proceeded directly in alcohol, without previous treatment with KOH, because the specimens have little musculature and the KOH can easily damage the larvae and eggs. It was made two transversal cuts, one in the curvature between segment III and IV, and another between the IV and VI. The first one allows to obtain the

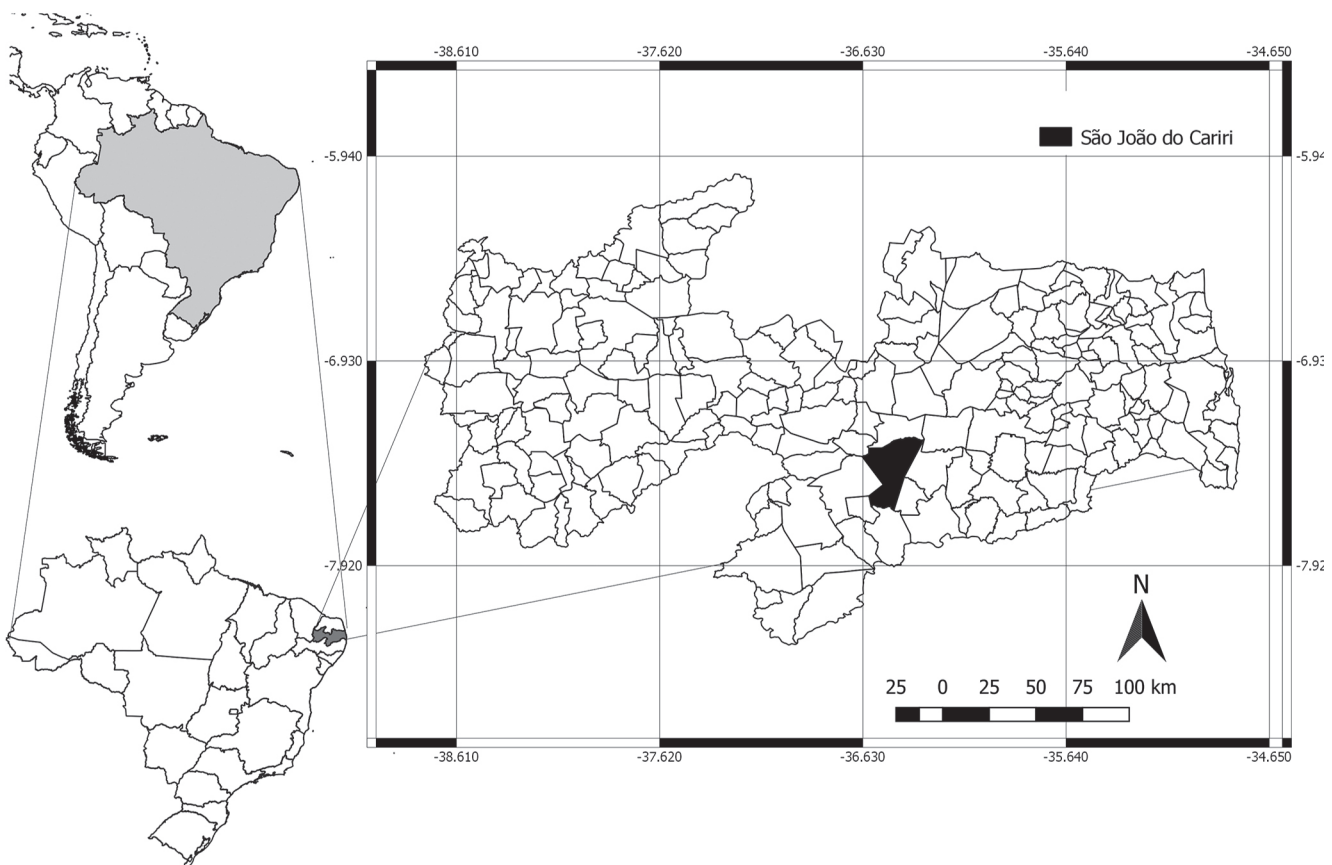


Figure 2. Estação Experimental São João do Cariri, located at São João do Cariri municipality, Paraíba State, northeastern of Brazil.

eggs usually found in segment IV and the second the larva or egg comprising the V and VI segments.

After removing the larvae and eggs, and sometimes the verification of presence of spermatheca, it was followed the methodology of Jacobson *et al.* (1986), the specimen was put in a cold 10% aqueous solution of KOH until the musculature being dissolved and keeping the cuticle intact. The photographs were made under a Carl Zeiss stereomicroscope Discovery. V12, with a camera attached to it.

RESULTS

The eggs are very large for all species and often quite easy to observe. They are filled with big veal globules, sometimes even deforming the membranous abdomen of the specimen. It was found that each specimen holds

at maximum three eggs into the abdomen. Two eggs are located side by side, filling whole segment IV, point of curvature of abdomen (Figs. 3A, C; 4A, B), and the third is always located at the apex of abdomen. Observations of specimens revealed that the development of the embryos is asynchronous: the egg located at the apex is the first to hatch a developed larva (Figs. 3B, 4B).

The larva hatches the egg and remains coiled with the most posterior part facing the apex of the abdomen (Fig. 3B). Some larvae were found without the thickest part of the egg and covered by a thin membrane which was presumed to be the vitelline membrane (Fig. 4B). The larva expelled through the genital orifice is in an advanced stage (Fig. 5) of that found inside abdomen, but none larval exuvia was found. Meanwhile, one of the two remaining eggs is already in a more advanced stage.

After the eclosion of the second egg, the larva gets to the apex of abdomen, in the same position as the first.

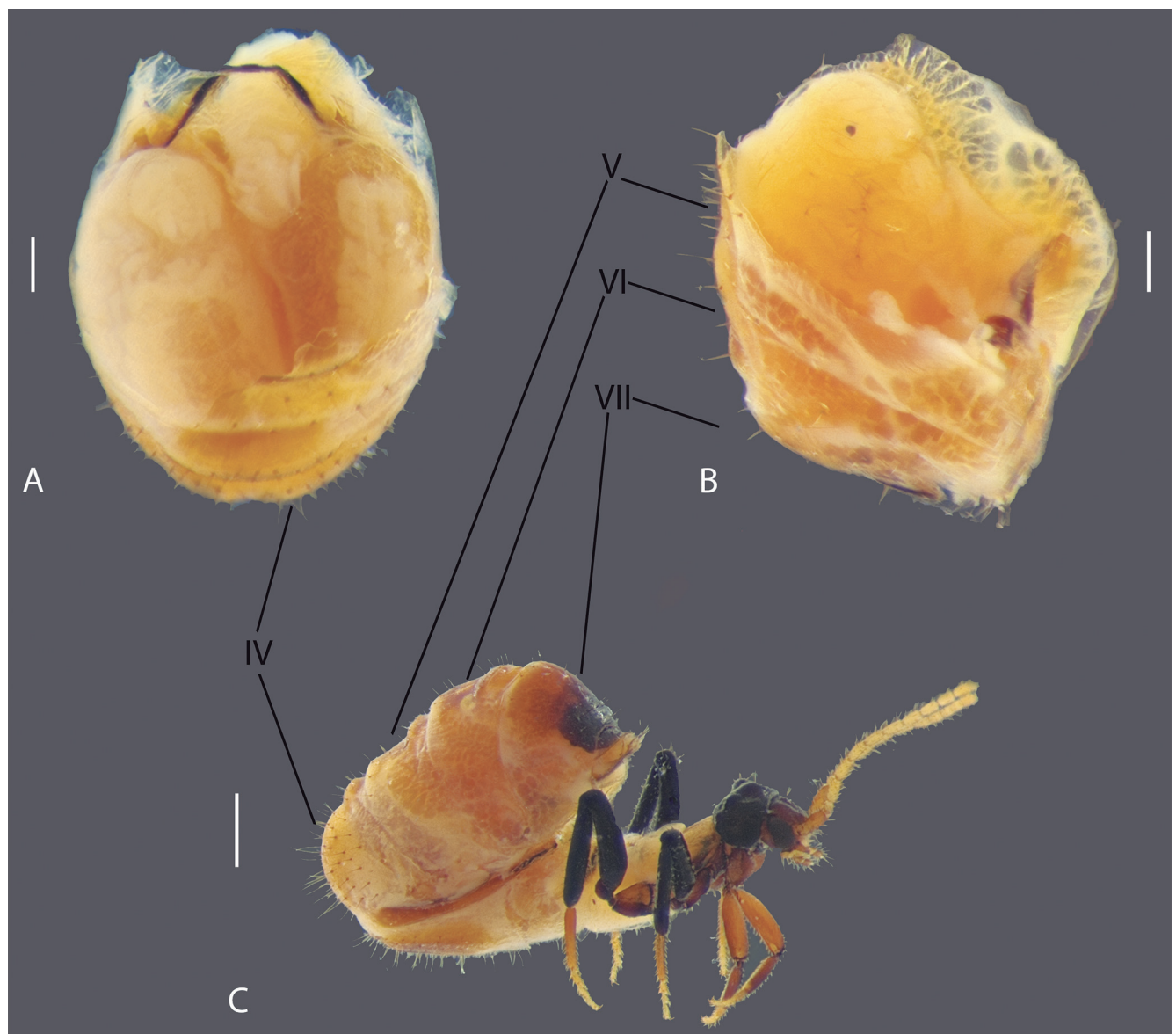


Figure 3. *Corotoca phylo* Schiødte, 1853, female (= paratype of *C. seeversi* Fontes, 1977). (A) transversal cut of curvature of the abdomen, with two exposed eggs, each with an embryo in different stage of development in relation to another; (B) transversal cut of abdomen from segment IV, with exposed larva; (C) habitus lateral. Scales: 0.5 mm.

Although it was recorded embryos with different stages of development (Figs. 3A; 4A), the larvae fully developed found in abdomen appear always to be in the same stage, which is possibly a previous stage of the larva expelled by female. No special nutritional structure was found in abdomen.

In the field, it was observed that the female of *Corotoca* spp. appears in the foraging trail and expels the larva only when the flow of termites is intense. Oliveira et al. (2018) observed that the female can move throughout a long distance, before stopping and expels the larva that was in abdomen apex. The expelled larva is initially covered with a membrane, which is ruptured while the larva is leaving the abdomen, before the female's deposition. When the act is finally successful, the posterior apex of the larva sticks on the head of the worker termite, as if some "glue" was involved in the process.

DISCUSSION

The results obtained from dissections and field observations are complementary and raise several hypotheses regarding to the life cycle of *Corotoca* species. The asynchronous development of the embryos is probably related to the fact of the female expels one larva each time when it leaves the nest for larviposition. The sequence in which the embryos develop begins with the larva of apex being the first to make room for each larva that would come from the base. According to Seevers (1957) supposition, the larva of *Corotoca* sp. become a pupa soon after leaving the female abdomen and at this moment it would be at an advanced stage of development. It was not clear if the larva observed by him was found outside or inside the female abdomen. His hypothesis may have been biased by the fact that larvae of *Corotoca* sp. had

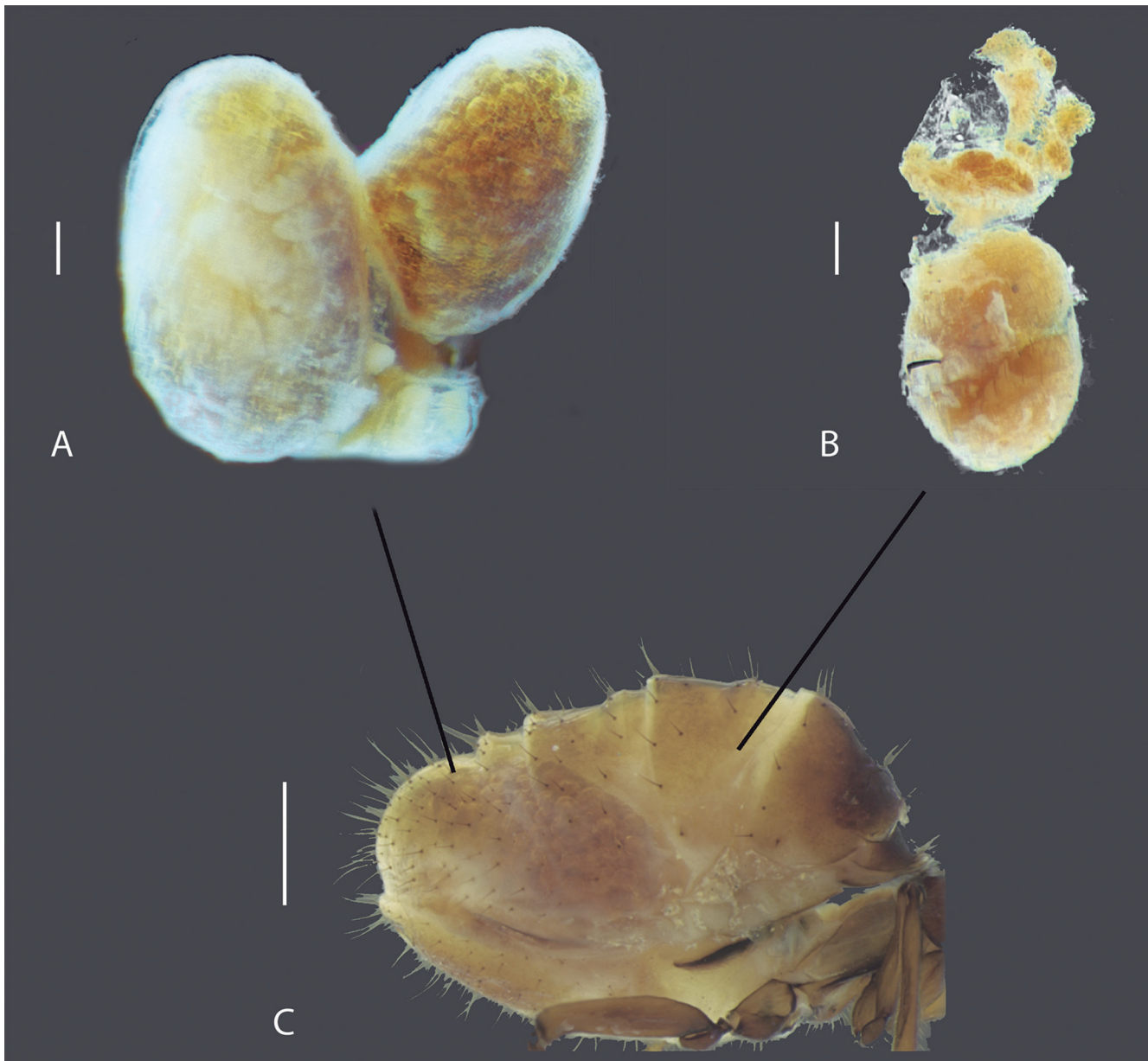


Figure 4. *Corotoca melantho* Schiødte, 1853, female. (A) eggs from segment IV, each with an embryo in different stage of development in relation to another; (B) larva found in the apex of abdomen; (C) abdomen of female, lateral view. Scales: 0.5 mm.



Figure 5. *Corotoca melantho* Schiødte, 1853, supposed second instar larva. Scale: 0.4 mm.

never been found in the nest of *Constrictotermes cyphergaster*, and this is at odds with Oliveira *et al.* (2018).

Despite of the instar of the larva found within the female's abdomen (probably first instar; L1) is not the same that the female expels on the foraging trail (probably second instar; L2), it is appropriate to raise a question: When does the larva found inside the female abdomen (probably L1) molts to the supposed L2, found after to be expelled by the female? Two hypotheses were raised to try to solve the issue: first, the larva molt inside the abdomen of the female and the exuvia is absorbed or expelled by female; or second, the molting occurs during the expelling of the larva. The second hypothesis is corroborated by the fact that, as commented before, no L2 larva was found in the abdomen, and by the supplementary material of Oliveira *et al.* (2018 – <https://zenodo.org/record/1208742#.W-iEoJNKi70>). In this material, specifically at the time that the larva is expelled, it appears to fidget in the sense that seems to try to leave behind the old exuvia. This issue, however, need to be better investigated to validate the hypothesis.

Regarding to the larviposition occurring when the termite flow is intense, we can consider that there is possibly visual mimicry in these termitophiles adults. This mimicry is responsible for deceiving predators in similar manner to that discussed by Kistner (1969) (see Wilson, 1971 for a different opinion on visual mimicry in termitophiles), which leads to the idea that perhaps leaving the nest with the trail crowded of termites helps to reduce the chance for termitophiles of being predated. Therefore, the mathematics of course would not be simple as hypothetically, "one female of *Corotoca* sp. leaving with 9 termites, the chance to be preyed is 1/10 and leaving with 99 it reduces to 1/100". Theorizing about why animals walk in groups, Hamilton (1971) indeed argued that it is advantageous to an individual to stick within a group when comes to avoid predation. The logic is that the predator would try to catch the closest prey, and the individuals in the group that are left in the edge, are more susceptible to predation.

The interesting information about the female of *Corotoca* sp. leaving the nest is that the path taken by the adult is always in the middle of the foraging trail. The workers even get out of the way when the *Corotoca* sp. fe-

male passes through it. Rarely two beetles are seen walking in the trail at the same time and it was observed an apparently carry of an adult beetle by a worker returning to the nest. This similar behavior was already described by Emerson (which was reported through Kistner, 1969), who observed *C. cavifrons* (Holmgren, 1910) carrying *Spirachtha mirabilis* Mann, 1923.

It is possible to claim that some reproductive strategies are better in increasing a progenitor's reproductive success than others – producing a higher number of descendants capable of surviving. Taking into account that natural selection not always find the "best" solution to a problem, maybe would be appropriate to address the following question: is the relatively very few occurrences of viviparity in insects a reflection of specific necessities of a few groups, or it is a "superior" strategy that could be able to achieve by a few groups and was unfeasible throughout evolutionary history for other lineages?

According to Williams (1996), the relatively few occurrences of viviparity in insects are because this strategy would reduce the fitness of most insect species. Then, rather than be an interesting strategy for most of the insects, it has adaptive value only in special circumstances. Williams said the circumstance was that for "those that have life histories that reduce availability or effectiveness of protected niches for the egg stage". If the termitophile's retention of eggs in abdomen represents a gain on reproductive success that extrapolate the relative fitness on other strategy like oviparity, the selection would be positive for viviparity condition. This case can be explained in demographic factors of growth and death rates of the young, and this scenario cited would be what Williams calls a "optimum shift towards viviparity".

The appearance of viviparity in termitophilous organisms as a possible reproductive strategy could be facilitated by the fact that those species lives inside a termite nest. Pismo *et al.* (2018) stated that the viviparity imply in prolonged periods of vulnerability while the physogastry and wing vestigialization should impair mobility. In this scenario, the adoption of a sedentary life style in termitaria could favour the fitness of this species. His hypothesis was reinforced by continuous spermatogenesis in this species leading to recurrent matings. The enclosed environment of termitaria could favor such behavior, once it increases the chances of encounters and matings. Nevertheless, wether it was product of the life in termitaria or an early feature remains inconclusive. The spermatheca in the genus *Corotoca* is notably smaller when compared to the possibly oviparous genus *Thyreoxenus* Mann, 1923. However, although others viviparous species in Coleoptera indeed do not have spermatheca, the relation of loss – or reduction – of spermatheca to viviparity, if any, is not clear.

In the description of the only known case of viviparity in Cerambycidae, Gabriš *et al.* (2016) take the absence of spermatheca, along with other features, as a clear indication of viviparity condition in the species. The authors explained that this phenomenon – loss of spermatheca – also happens in viviparous chrysomelids. However, it is interesting to note that, as punctuated by Bontems

(1984), not only viviparous chrysomelids have spermatheca absent, but also some oviparous chrysomelids. Therefore, according to the author, there is possibly no relation between the loss of spermatheca and the viviparous condition. The loss of spermatheca and its relation to the natural history of the species needs to be better evaluated in future studies.

The Williams' (1996) hypothesis on the reason biological groups developed the viviparous condition along their evolutionary history, has a logic that take into account the relatively fitness of this strategy compared

to the oviparous one. The central point is to protect the immature in a stage that it would not be successful if its development occurred outside the female body. Seevers (1957) after studying of larvae of several species of the genus *Thyreoxenus*, that were found in termite nests, inferred that this genus is oviparous. In addition to the fact that no larva has been found in female abdomen, his argument is reinforced by presence of exudative structures in the immatures. So, this author concluded that the viviparity condition in *Corotoca* and *Spirachtha* is an adaptative strategy resulted by a selective pressure

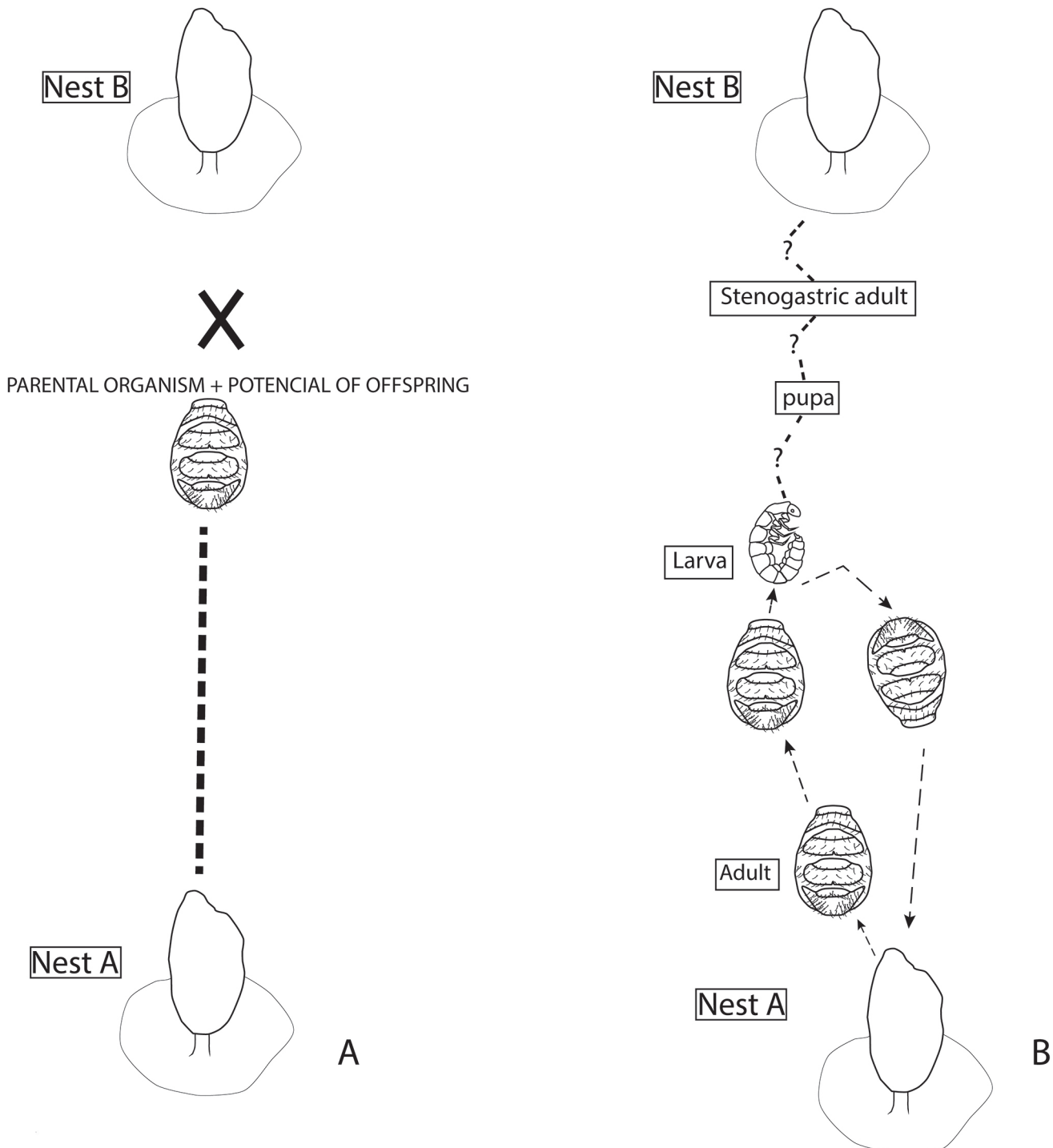


Figure 6. Scheme illustrating part of the life cycle of *Corotoca* sp. Left (A) shows hypothetical case of dispersion made by the adult, while the right (B) illustrates the hypothesis proposed in this work, of dispersion mainly by immature.

from the absence of those structures. The problem with Seevers' argument is that, although relatively few larval stages are known for *Corotocini*, most of them seems to have no evidence for viviparity and also exudative structures. This is true for immatures of *Termitoptochus luzonicus* Silvestri, 1921, *T. peninsularis* Silvestri, 1921, *T. sumatranus* Silvestri, 1921, *Termitoptocinus australiensis* Silvestri, 1921. *Affinoptochus exclus* Kistner, 1982 and *Eutermitoptochus novae* Silvestri, 1921 (Silvestri, 1921; Kistner, 1982). The exception is for *Paracorotoca* which has several exudative structures.

Despite this criticism, indeed there are two evolutionary routes by which a termitophile can follow to protect its offspring from suffering any damage that compromises its survival in the host nest. One is to ensure that its offspring have adaptations that avoid it from damage while in the nest, whether biochemical, morphological or behavioral adaptations. The other route is to postpone the time that the immature would be exposed to external risks, guaranteeing their development within the female abdomen, that is, viviparity. In *Corotoca* species, the viviparity apparently does not only function as a protective strategy in delaying the larviposition due a stage of risk for the immature, but is also a strategy of dispersion, allowing the female to carry the immature to the foraging trail at a very specific time. A question that can be asked is this: a better strategy, fitness, just to take care of the larvae inside the nest?

The behavior observed in *Corotoca* along with the data obtained from internal anatomy, can be a supposed improvement of the fitness of the species. It is a fact that dispersion must occur on one way or another. If we hypothesize an adult female trying to disperse from nest A to B, but the attempt was unsuccessful as a predator interrupted its path, not only the parental organism is lost, but as well all the offspring potential it carries (Fig. 6A). Then, the strategy adopted in the genus *Corotoca* is the larva, one at a time (at least three times total) to be deposited on the foraging trail and carried by termites, that the chance of success in dispersion increases and the loss, when it occurs, affects only one individual of the offspring, not all of it (Fig. 6B).

The strategy of expelling one larva at time, with intervals between births could mean two adaptations: first, if the female gave birth to the three larvae at the same time, they would be close to each other and could be predated by a single predator; and second, considering that the larvae detect the chemical trail of termites, without discriminating nests, this interval between births would prevent the same larvae from reaching the same nests.

ACKNOWLEDGMENTS

To Sônia A. Casari for the careful reading and suggestions to the manuscript. To Edilson Caron (UFPR) and Alfred Newton (FMNH) for providing preliminary bibliography for this work. The first author also thanks Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES) for the financial support.

Contributions statement: All authors contributed equally.

Disclosure statement: No potential conflict of interest was reported by the authors.

REFERENCES

- Araujo, K.D. 2005. *Variabilidade temporal das condições climáticas sobre as perdas de CO₂ na encosta do açude Namarados, em São João do Cariri, PB.* (Masters Dissertation). Areia, Universidade Federal da Paraíba. 101p.
- Barbosa, M.R.V.; Lima, I.B.; Lima, J.R.; Cunha, J.P.; Agra, M.F. & Thomas, W.W. 2007. Vegetação e Flora no Cariri Paraibano. *Oecologia Brasiliensis*, 11: 313-322.
- Blackburn, D. & Evans, H. 1986. Why are there no Viviparous Birds? *The American Naturalist*, 128(2): 165-190.
- Bontems, C. 1984. La viviparité chez les Chrysomelinae (Col.). *Bulletin de la Societe entomologique de France*, 89: 973-981.
- Brisout de Barneville, C. 1860. Descriptions de quelques coléoptères nouveaux propres à la faune française et spécialement aux environs de Paris. *Annales de la Société entomologique de France*, 8(3): 339-350.
- Carayon, J. 1962. La viviparité chez les Hétéroptères. In: Internationaler Kongress für Entomologie, Wien, 11^o. *Verhandlungen*. Wien, 1960. v. 1, p. 711-714.
- Clutton-Brock, T. & Scott, D. 1991. *The evolution of parental care*. Princeton, Princeton University Press, 368p.
- Dawkins, R. 2011. *The tyranny of the discontinuous mind*. [online] Newstatesman.com. Available at: <https://www.newstatesman.com/blogs/the-staggers/2011/12/issue-essay-line-dawkins>. Access in: 10/10/2017.
- Donisthorpe, H. 1917. Myrmecophilous notes for 1916. *Entomologist's Record*, London, 29(3): 48-52.
- Donisthorpe, H. 1926. Viviparity of *Lomechusa strumosa* F. *The Entomologist's Monthly Magazine*, 62: 21.
- Dutrillaux, A.; Pluost-Sigwalt, D & Dutrillaux, B. 2010. (Ovo-)viviparity in the darkling beetle, *Alegoria castelnaui* (Tenebrioninae: Ulomini), from Guadeloupe. *European Journal of Entomology*, 107(4): 481-485.
- Fabricius, J.C. 1775. *System Entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Flensburgi et Lipsiae, Officina Libraria Kortii. 850p.
- Fenyés, A. 1918. *Coleoptera: Family Staphylinidae, subfam. Aleocharinae*. In: Wytzman, P. *Genera Insectorum*. Bruxelles, V. Verteneuil & L. Desmet. 110p.
- Fleming, J. 1821. *Insecta. Supplement to the fourth, fifth and sixth editions of the Encyclopaedia Britannica, with preliminary dissertations on the history of the sciences*. Edinburgh, Archibade Constable Co. v. 5, p. 41-56.
- Fontes, L.R. 1977. Notes on the termitophilous genus *Corotoca*, with a new species from Brazil (Coleoptera, Staphylinidae). *Revista Brasileira de Entomologia*, 21(3/4): 69-74.
- Gabriš, R.; Kundrata, R & Trnka, F. 2016. Review of *Dolichostyrax Aurivillius* (Cerambycidae, Lamiinae) in Borneo, with descriptions of three new genera and the first case of (ovo)viviparity in the long-horned beetles. *ZooKeys*, 587: 49-75.
- Glaçon-Deleurance, S. 1963. Recherches sur les Coléoptères troglobies de la sous-famille des Bathysciinae. *Annales des Sciences Naturelles, Zoologie et Biologie Animale*, Paris, 12 Serie, 5(1): 1-172.
- Hagan, H. 1948. A Brief Analysis of Viviparity in Insects. *Journal of the New York Entomological Society*, 56(1): 63-68.
- Hagan, H. 1951. *Embryology of the viviparous insects*. New York, Ronald Press.

- Hölldobler, B.; Kwapich, C.L. & Haight, K.L. 2018. Behavior and exocrine glands in the myrmecophilous beetle *Lomechusoides strumosus* (Fabricius, 1775) (formerly called *Lomechusa strumosa*) (Coleoptera: Staphylinidae: Aleocharinae). *Plos One*, 13(7):e0200309.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, 31(2): 295-311.
- Holmgren, N. 1910. Versuch einer Monographie der amerikanischen Eutermes-Arten. *Mitteilungen aus dem Naturhistorischen Museum*, 27: 171-325.
- Iwan, D. 2000. Ovioparity in tenenbrionid beetles of the melanocratoid Platynotina (Coleoptera: Tenebrionidae: Platynotini) from Madagascar, with notes on the viviparous beetles. *Annales Zoologici*, Warszawa, 50(1): 15-25.
- Jacobson, H.R.; Kistner, D. & Pasteels, J.M. 1986. Generic revision, phylogenetic classification, and phylogeny of the termitophilous tribe Corotocini (Coleoptera: Staphylinidae). *Sociobiology*, 12: 1-245.
- Jordan, K.H. 1913. Zur Morphologie und Biologie der myrmecophilen Gattungen *Lomechusa* und *Atemeles* und einiger verwandter Formen. *Zeitschrift für Wissenschaftliche Zoologie*, 107(2): 346-386.
- Kistner, D. 1969. The biology of termitophiles. In: Krishna, K. & Weesner, M (Eds.). *Biology of Termites*. New York, Academic Press. p. 525-557.
- Kistner, D. 1970. Revision of the Old-World species of the termitophilous tribe Corotocini (Coleoptera: Staphylinidae). III. The genera *Idiogaster*, *Paracorotoca*, and *Fulleroxenus*, with notes on the relationships of their species, postimaginal growth, and larvae. *Journal of the Entomological Society of Southern Africa*, 33: 157-192.
- Kistner, D. 1976. Notes on the behavior of the termitophilous Staphylinidae associated with *Trinervitermes trinervoides* (Sjoestedt) or an explanation of the cover (Coleoptera; Isoptera: Termitidae, Nasutitermitinae). *Sociobiology*, 2(1): 96-102.
- Kistner, D. 1982. Termitophilous Aleocharinae Associated with *Nasutitermes matangensis* in Java, Republic of Indonesia (Coleoptera, Staphylinidae). *Sociobiology*, 7(2): 213-244.
- Liebherr, J. & Kavanaugh, D. 1985. Ovioparity in carabid beetles of the genus *Pseudomorpha* (Insecta: Coleoptera). *Journal of Natural History*, 19(6): 1079-1086.
- Mann, W.M. 1923. New genera and species of termitophilous Coleoptera from Northern South America. *Zoologica*, New York, 3(17): 323-366.
- Meier, R., Kotrba, M., Ferrar, P. 1999. Ovioparity and viviparity in the Diptera. *Biological Reviews of the Cambridge Philosophical Society*, 74(3): 199-258.
- Newton, A.F. 2017. Nomenclatural and taxonomic changes in Staphyliniformia (Coleoptera). *Insecta Mundi*, 0595: 1-52.
- Oliveira, M.H.; Vieira, R.V.S.; Moreira, I.E.; Pires-Silva, C.M.; Lima, H.V.G.; Andrade, M.R.L. & Bezerra-Gusmão, M.A. 2018. "The road to reproduction": foraging trails of *Constrictotermes cyphergaster* (Termitidae: Nasutitermitinae) as maternities for Staphylinidae beetles. *Sociobiology*, 65(3): 531.
- Pisno, R. M.; Salazar, K.; Lino-Neto, J.; Serrão, J. E. & DeSouza, O. 2018. Termitariophily: expanding the concept of termitophily in a physogastric rove beetle (Coleoptera: Staphylinidae). *Ecological Entomology*. DOI
- Schiødte, J.M.C. 1853. On some Staphylinidae, found in the nests of termites. *Proceedings of the Zoological Society of London*, 21: 101-102.
- Schiødte, J.M.C. 1856. Observations sur des Staphylins vivipares qui habitent chez les Termites. *Annales Sciences Naturelles Zoologie et Biologie Animale*, 5: 169-183.
- Seevers, C.H. 1957. A monograph on the termitophilous Staphylinidae (Coleoptera). *Fieldiana: Zoology*, 40: 1-334.
- Sellier, R. 1955. La viviparité chez les insectes. *Année Biologique*, Paris, 31: 525-545.
- Silvestri, F. 1901. Nota preliminare sui Termitidi sud-americani. *Bollettino dei Musei di Zoologia ed Anatomia Comparata della Reale Università di Torino*, 16(389): 1-8.
- Silvestri, F. 1921. Descrizione di alcuni Staphylinidae termitofili delle regioni orientale e australiana. *Bollettino del Laboratorio di zoologia generale e agraria della R. Scuola superiore d'agricoltura in Portici*, 15(1): 3-23.
- Tschinkel, W. 1978. Ovioparity in some tenebrionid beetles. *The Coleopterists Bulletin*, 32(4): 315-317.
- Warren, E. 1914. Notes on the occurrence in South Africa of a termitophilous beetle of the genus *Corotoca*. *Annals of the Natal Museum*, 3: 103-106.
- Warren, E. 1920. Observations on the comparative anatomy of the termitophilous Aleocharine *Paracorotoca Akermani* (Warren). *Annals of the Natal Museum*, 4: 297-366.
- Wasmann, E. 1915a. Neue Beiträge zur Biologie von *Lomechusa* und *Atemeles*. *Zeitschrift für Wissenschaftliche Zoologie*, 114: 251-396.
- Wasmann, E. 1915b. Viviparität und Entwicklung von *Lomechusa* und *Atemeles*. *Wiener Entomologische Zeitung*, 34: 382-393.
- Weber, H. 1933. *Lehrbuch der Entomologie*. Jena, Gustav Fischer Verlag. 726p.
- Williams, G.C. 1996. *Adaptation and Natural Selection: a critique of some current evolutionary thought*. Princeton, Princeton University Press. 320p.
- Wilson, E.O. 1971. *The Insect Societies*. Cambridge, Harvard University Press. 562p.
- Zilberman, B. 2018. New species and synonymy in the genus *Corotoca* Schiødte, 1853 (Coleoptera, Aleocharinae, Corotocini). *Zootaxa*, 4434(3): 547-560.
- Zilberman, B. & Casari, S.A. 2018. New species of *Corotoca* Schiødte, 1853 from South America and description of first instar larva. *Zootaxa*, 4527(4): 521-540.