



CARLOS MORENO PIRES SILVA

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**Cladistic analysis, taxonomic revision & biological notes of the termitophilous genus *Xenogaster* Wasmann, 1891 (Staphylinidae, Aleocharinae, Corotocini)**

**Análise cladística, revisão taxonômica & notas de biologia do gênero termitófilo *Xenogaster* Wasmann, 1891 (Staphylinidae, Aleocharinae, Corotocini)**

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Single Volume

São Paulo  
2024

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Dissertation submitted to the Graduate Program of the Museu de Zoologia da Universidade de São Paulo in partial fulfillment of the requirements for the degree of Master of Science (Systematics, Animal Taxonomy and Biodiversity).

**Advisor:** Profa. Dra. Sônia A. Casari

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## NOTICE

This dissertation is a partial requirement for the Master degree in Systematics, Animal Taxonomy and Biodiversity, and, as such, should not be considered as a publication in the sense of the article 9 of ICZN – Internacional Comission on Zoological Nomenclature. Therefore any nomenclatural act related to it should not be considered.

## AVISO

Essa dissertação é parte dos requerimentos necessários à obtenção do título de mestre em Sistemática, Taxonomia Animal e Biodiversidade, e como tal, não deve ser vista como uma publicação no sentido do artigo 9 do Código de Nomenclatura Zoológica da "ICZN – Internacional Comission on Zoologica Nomenclature". Desta forma, não devem ser considerados quaisquer atos nomenclaturais a ela relacionados.

PIRES-SILVA, Carlos M.

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*"I would have gotten away with it if it hadn't been for the scientists... who were so bold as to publish an exposé of my true identity! [...] What's a free meal or two in a colony of millions of termites? Other rove beetles have pulled off this infiltration with a lot more bloodshed. At least 12 species of parasitic rove beetles have evolved to resemble army ants. They smell like them, act like them, and even set out on raids with them. And yet these beetles do not receive free meals of mouth juice. These beetles eat their neighbors' babies—tiny eggs and soft larvae of ants that will not live long enough to know leg. I would never impose my own subjective notions of morality on others, but, c'mon, this makes my free regurgitated smoothies look pretty good in comparison!"*

The (very angry) rove beetle *Austrospirachtha carrioi* in his interview to **Defector**.

## RESUMO

*Xenogaster* Wasmann, 1891 é um gênero exclusivamente Neotropical de besouros termitófilos associados aos cupins dos gêneros *Nasutitermes* Dudley, 1890 e *Cortaritermes* Mathews, 1977. Neste estudo, realizou-se uma análise cladística e uma revisão taxonômica do gênero, que previamente incluía 10 espécies conhecidas. A análise cladística incluiu 27 terminais (14 do grupo interno e 13 do grupo externo) e 135 caracteres morfológicos, que foram derivados do exame de estruturas tanto externas quanto internas. A análise com pesagem implícita resultou em uma árvore filogenética mais parcimoniosa com 419 passos. Esta topologia sustentou a monofilia do gênero *Xenogaster*, com suporte em 7 transformações, incluindo duas sinapomorfias exclusivas. Adicionalmente, identificaram-se duas novas espécies, *Xenogaster utopica* **sp. nov.** e *X. rochai* **sp. nov.**, com base no estudo morfológico. Um novo gênero, *Paraxenogaster* **gen. nov.**, foi criado para acomodar uma espécie anteriormente descrita no gênero *Xenogaster*, sendo proposta a nova combinação *Paraxenogaster fossulata* **comb. nov.**. Além disso, a análise cladística revelou que a espécie *Xenogaster mexicana* Kistner & Jacobson, 1976 pertence ao gênero *Trachopeplus* Mann, 1923, sendo proposta a nova combinação *T. mexicanus* **comb. nov.**. Os dois gêneros, *Xenogaster* e *Paraxenogaster*, juntamente com as 13 espécies, foram minuciosamente descritos ou redescritos, ilustrados e incluiu-se chaves de identificação para o gênero *Xenogaster* e para os gêneros Neotropicais da subtribo Termitogastrina, à qual *Xenogaster* pertence. Adicionalmente, o fenômeno do crescimento pós-imaginal em *Xenogaster* foi discutido com base em espécimes coletados em diferentes estágios de desenvolvimento de fisogastría.

**Palavras-Chave:** Sistemática. Neotropical. Termitofilia. Fisogastría. Homologia primária.

## ABSTRACT

*Xenogaster* Wasmann, 1891, is an exclusively Neotropical genus of termite-associated beetles, which are associated with termites of the genera *Nasutitermes* Dudley, 1890, and *Cortaritermes* Mathews, 1977. In this study, a cladistic analysis and taxonomic revision of the genus were conducted, which previously included 10 known species. The cladistic analysis encompassed 27 terminals (14 from the ingroup and 13 from the outgroup) and 135 morphological characters derived from an examination of both external and internal structures. The analysis, using implicit weighting, resulted in a more parsimonious phylogenetic tree with 419 steps. This topology supported the monophyly of the genus *Xenogaster*, with the support of 7 transformations, including two exclusive synapomorphies. Furthermore, two new species, *Xenogaster utopica* **sp. nov.** and *X. rochai* **sp. nov.**, were identified based on morphological studies. A new genus, *Paraxenogaster* **gen. nov.**, was established to accommodate a species previously described in the genus *Xenogaster*, and the new combination *Paraxenogaster fossulata* **comb. nov.** was proposed. Additionally, the cladistic analysis revealed that the species *Xenogaster mexicana* Kistner & Jacobson, 1976 belongs to the genus *Trachopeplus* Mann, 1923, resulting in the new combination *T. mexicanus* **comb. nov.** Both genera, *Xenogaster* and *Paraxenogaster*, along with the 13 species, were thoroughly described or redescribed, illustrated, and identification keys for the genus *Xenogaster* and the Neotropical genera of the subtribe Termitogastrina, to which *Xenogaster* belongs, were provided. Furthermore, the phenomenon of post-imaginal growth in *Xenogaster* was discussed based on specimens collected at several stages of development of physogastry.

**Keywords:** Systematics. Neotropical. Termitophily. Physogastry. Primary homology.

# Contents

<b>General Introduction</b>	<b>15</b>
<b>General References</b>	<b>26</b>
<b>1 Cladistic analysis and taxonomic revision of the termitophilous genus <i>Xenogaster</i> Wasmann, 1891 (Staphylinidae, Aleocharinae, Corotocini)</b>	<b>33</b>
1.1 Introduction . . . . .	34
1.2 Conclusions . . . . .	36
<b>References</b>	<b>37</b>
<b>2 Exploring post-imaginal growth phenomena in <i>Xenogaster</i> Wasmann, 1891 (Coleoptera: Staphylinidae: Corotocini)</b>	<b>42</b>
2.1 Introduction . . . . .	43
<b>References</b>	<b>45</b>
<b>3 General Conclusions</b>	<b>47</b>
<b>General Conclusions</b>	<b>47</b>

# List of Abbreviations

<b>EWPC</b>	Erich Wasmann Private Collection
<b>FMNH</b>	Field Museum of Natural History
<b>KU</b>	Kansas University
<b>LRF</b>	Luiz Roberto Fontes Private Collection
<b>MZSP</b>	Museu de Zoologia da Universidade de São Paulo
<b>USNM</b>	Smithsonian National Museum of Natural History

# General Introduction

*"From street to street he piped advancing, and step for step they followed dancing" - Pied Piper of Hamelin, Robert Browning (1842)*



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Symbiosis, a fundamental ecological concept, pertains to the intricate interactions and close relationships established between two or more distinct biological organisms from different species, often resulting in mutually beneficial outcomes (Margulis, 1971; Smith et al., 1987). These interactions play a pivotal role in shaping ecosystems and driving evolutionary processes (Ricklefs et al., 2014). Symbiotic relationships are categorized into three main types: mutualism, where both species involved derive benefits; commensalism, where one species benefits while the other remains unaffected; and parasitism, where one species benefits at the expense of the other (Ricklefs et al., 2014).

Most of symbiotic relationships are parasitic, and parasitism is considered one of the best strategies among species (Poulin and Morand, 2000). This kind of interaction, however, was seen by many ecologists only with medical purposes (Hughes et al., 2012), but in the



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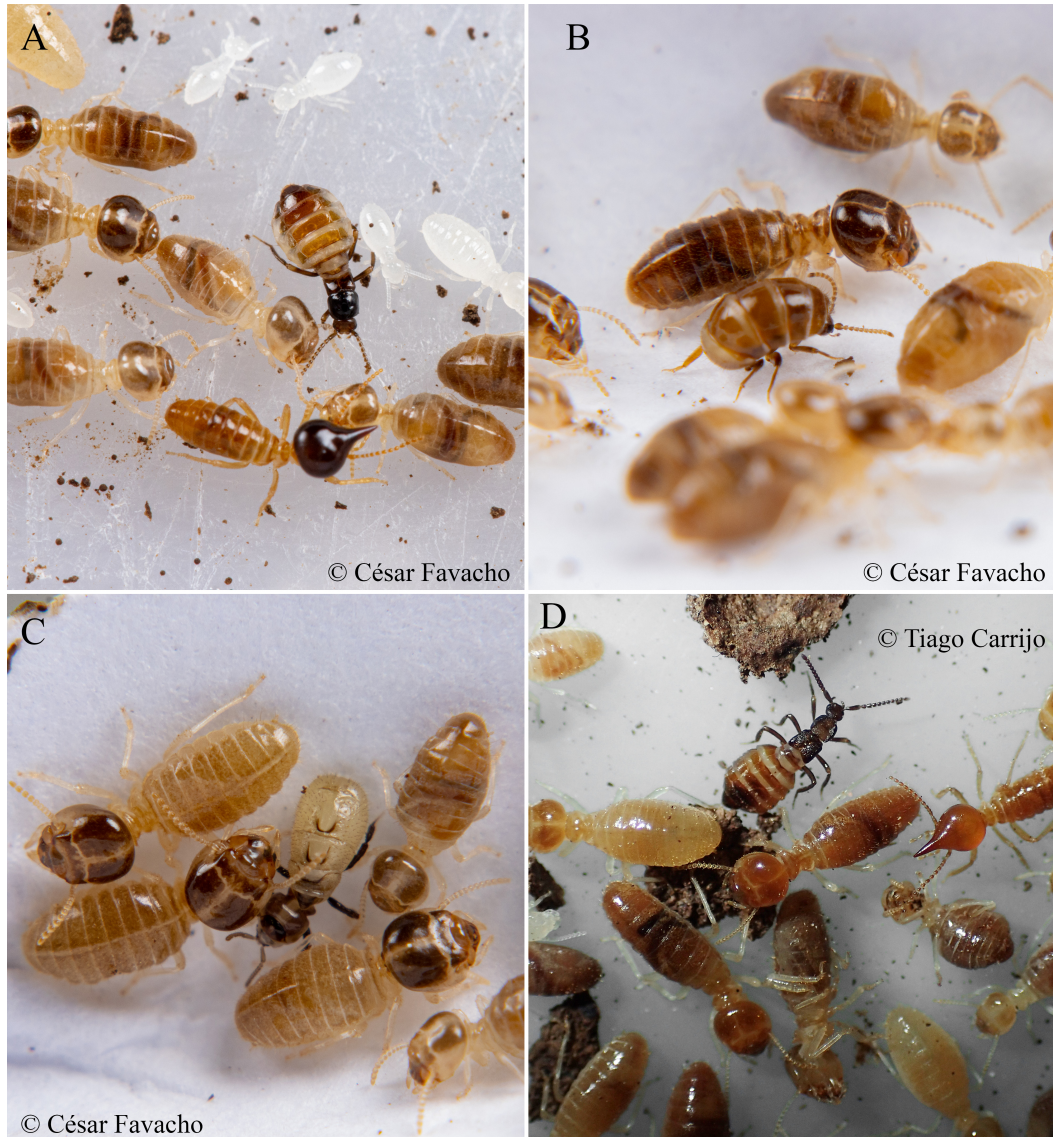
late 1970, this kind of thinking starts to change when several scholars noticed that parasites could be seen as true models for understanding the evolutionary processes (Pojmanska et al., 1967; Bakke, 1976; Hughes et al., 2012). Interactions displayed between hosts and parasites, where at the same type that a given host species develops mechanisms to avoid parasites, which on the other hand are guided through the pressures imposed by their hosts to overcome such barriers, is a true evolutionary armed race (Dawkins and Krebs, 1979). Moreover, with further evidence that parasites have ecological, evolutionary and behavioral significance (Poulin et al., 2005; Thomas et al., 2010; Poulin and Maure, 2015), host-parasite interactions are also regarded as one of the ideal systems for the study of coevolution (Smyth, 1969; Anderson and May, 1982; Ebert, 2008; Gandon et al., 2008).

Colonies of eusocial insects (ants, wasps, bees, and termites) are known to harbor, and coevolve, with a great diversity of obligatory parasites, including fungi (Hyodo et al., 2003), nematods (Kanzaki et al., 2019), crustaceans (Lisboa et al., 2013), mites (Pisno et al., 2023), and others (Kistner, 1979). Termites specifically are constant threatened by the invasion of social parasites, individuals which do not merely target a single termite but instead impact the entire colony (Kistner, 1982b; Holldobler and Wilson, 2009; Carvalho, 2018). Some of them, live in obligatory association with termites colonies, and those obligatory inquilines are called "termitophiles" (Kistner, 1969). The name likely originates from the fusion of the words "termite" (derived from Latin "termes", meaning "woodworm") and "phílos" (indicating "beloved"), highlighting the profound relationship these organisms displays toward termites.

The general definition of "termitophile" is any organism, other than a termite, that lives at least one part of their life cycle in complete dependence of the termite colony (Kistner, 1969). This definition also eliminates organisms that are using the termite nests only as a shelter (called termitariophiles). However, why such state of *dependency* would confer any advantage? Termites species stand as remarkable examples of natural engineers. Their nests are intricately designed structures, a true regulated environment characterized by stable temperature and humidity levels (Noirot and Darlington, 2000; Singh et al., 2019). Moreover, these nests are a physical fortress against potential predators (Redford, 1984). Lastly, the relatively reduced threat posed by certain termite species, when compared to, for instance, the highly efficient colony defense mechanisms observed in ants (Higashi and Ito, 1989; Heil and McKey, 2003), is complemented by the presence of a substantial population of immature individuals within the termite nests, as well as the presence of fungus gardens in some species (Thorne, 1985; Wisselink et al., 2020). These features collectively render termite nests a rich reservoir of resources, enticing a diverse array of opportunistic (or obligatory) species.

Nonetheless, nest builder species in termites exhibit mechanisms to avoid invasion by their social parasites (Clément and Bagnères, 2019). On the other hand, invaders develop

strategies to bypass unnoticed by termites (Hugo et al., 2020). These strategies, encompassing tactics such as chemical (Rosa et al., 2018) or morphological similarity (Matsuura, 2006), have demonstrated their selective advantage, yielding secondary benefits in the form of nestmate care (Pires-Silva et al., 2022), or visual mimicry (Fig. 1) (Zilberman and Pires-Silva, 2023).



**Figure 1:** Morphological diversity across specimens of Corotocini with a supposedly visual mimicry with their termites hosts. (A), *Termitogaster* cf. *emersoni* Mann (Termitogastrina); (B), *Termitophya* sp. (Abrotelina); (C), *Thyreoxenus alakazam* Pires-Silva, Zilberman & Eloi (Corotocina); (D), *Xenogaster subnuda* Seevers (Termitogastrina).

The advent of termitophily traces back to the mid-19th century. The Danish zoologist Johannes Theodor Reinhardt embarked on an expedition to Brazil on behalf of the Royal

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Museum of Natural History, Belgium. In 1852, he collected specimens in termite nests<sup>1</sup> from Lagoa Santa, Minas Gerais, where he had been assisting the father of Brazilian paleontology, Peter Wilhelm Lund with his paleontological research.

These particular specimens were later sent to his colleague, the Danish entomologist Jørgen Matthias Christian Schiødte, who in the year 1853, undertook the task of documenting the findings of the expedition. His resulting publication marked a turning point in the Proceedings of the Zoological Society of London and entomology as well, as it unveiled the first comprehensive report of other insects living within termite nests (Schiødte, 1853). These insects, specifically beetles, were referred to as "strangers" within the Staphylinidae family, and the author classified them into two distinct genera: *Corotoca* and *Spirachtha* (Schiødte, 1853). His observations led to the establishment of termitophily as a novel scientific field.

Schiødte's reaction to the unique morphology of these beetles was evident, as he referred to their abdomen as "constructed in a most extraordinary manner, being membranaceous, of an enormous size" (Schiødte, 1853). This statement referred to the enlargement of membranous portions of the abdomen, and sometimes the thorax, a condition known as physogastry (Audy et al., 1972).

Since Schiødte's pioneering work, numerous termitophilous species from several groups of arthropods have been described, and this habit is believed to have independently evolved between 29 and 40 times (Kistner, 1969, 1979, 1982a). Coleoptera, as the most diverse order, presents termitophily documented in at least 20 families, with greater selectivity within the family Staphylinidae (rove beetles), where it has arisen independently at least 12 times (Kistner, 1969, 1982a). This selectivity is even more pronounced in Aleocharinae, with 11 independent occurrences, with evidence that this habit arose at least around 99 million years ago, in the mid-Cretaceous period (Cai et al., 2017; Jiang et al., 2021).

### Why do rove beetles "love" termitophily?

The family Staphylinidae Latreille, 1802, commonly known as rove beetles, are primarily identified by their minute size and reduced elytra, which expose a significant portion of the abdomen (Betz et al., 2018). They constitute the group of organisms with the largest number of described species in the planet, approximately 66,928 (Newton, 2022), and are distributed on all continents and major islands, except Antarctica (Thayer, 2016), occupying a wide array of ecological niches such as detritivores (Teixeira et al., 2009), predators (Stocker et al., 2022), fungivores (Ashe, 1990), or saproxylic (Staniec et al., 2018).

Within Staphylinidae, the subfamily Aleocharinae stands out as the most diverse, with approximately 16,864 described species (Newton, 2022). Previous studies have supported the monophyly of the subfamily based on morphological characters in both adults and larvae (Ashe, 1990, 1991). More recently, new evidences have confirmed the monophyly of

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<sup>1</sup>The termites were later identified as *Constrictotermes cyphergaster* (Silvestri, 1901)

Aleocharinae (Orlov et al., 2021a), relying on both morphological and molecular datasets. Orlov and collaborators (2021a) recovered the monophyletic group (Habrocerinae + Trichophyinae) as a sister to all Aleocharinae, and within the subfamily, the monophyletic tribe Gymnusini emerged as a sister group to the remaining Aleocharinae taxa. The majority of aleocharine species are small predators, and yet they represents the most diverse known lineage to coevolve with ants and termites (Maruyama and Parker, 2017). This close association may indicate a high degree of symbiosis between aleocharines and these social insects, since close interactions between them were exhaustively reported (Kistner, 1969; Maruyama and Parker, 2017; Pires-Silva et al., 2022; Żyła et al., 2022).

But, why in Aleocharinae? What makes those beetles so good at “adopting” a termitophilous lifestyle? Alternatively, why has natural selection favored this specific habit within this group of beetles? We can try to answer these questions by looking deep into a group of rove beetles which are associated with ants colonies, known as myrmecophiles. Similar to termitophiles, the rove beetles associated with ants exhibit a remarkable array of morphological adaptations that closely resemble their ant hosts, often to the point of being nearly indistinguishable (Maruyama and Parker, 2017). The exploitation of resources from eusocial colonies was so advantageous that myrmecophilous aleocharines have independently evolved a myrmecoid body shape at least 12 times, thereby anatomically mimicking and deceiving their hosts (Maruyama and Parker, 2017).

The secret of such success, and “facility” to adopt this parasitic lifestyle, according to Parker et al. (2017), is probably due to two factors: (i) the aleocharinae body plan, and (ii) chemical innovations. Unlike many other Coleoptera species, in which the elytra fully cover the abdomen, thereby limiting segment mobility, most staphylinids have an exposed abdomen. In aleocharines, however, the abdomen also serves as a vital interface between the beetle and its host organisms (Parker et al., 2017). Therefore, the shortened elytra increased the abdominal flexibility, facilitating the reconfiguration in some species, and enabling them to adopt anatomical shapes that closely resemble their host ants and termites (Fig. 2) (Seev-ers, 1957; Kistner, 1979; Parker, 2016; Maruyama and Parker, 2017; Parker et al., 2017; Zilberman and Pires-Silva, 2023).

A noteworthy synapomorphy of the Aleocharinae is the presence of a tergal gland on the anterior margin of abdominal segment VII which is also associated with the “manipulative behavior” displayed by myrmecophiles and termitophiles toward their hosts, often appeasing them (Fig. 3) (Kistner, 1969; Hölldobler et al., 2018; Pires-Silva et al., 2022). Moreover, aleocharine taxa have evolved glands in addition to the tergal gland (Kistner, 1982b; Zilberman, 2020; Pires-Silva et al., 2022; Parker, 2016; Parker et al., 2017). As a result, glandular openings on the exposed abdomen come into direct contact with ants (or termites) leading to a glandular and chemical evolution.

Consequently, this preadaptative groundplan of morphological and chemical features, led



**Figure 2:** *Austrospirachtha carrioi* Zilberman & Pires-Silva. (Aleocharinae: Corotocini). Lateral (A), and dorsal (B) views. The genus *Austrospirachtha* is known for its highly developed physogastry and mimicry adaptations. Photo Credits: ©Bruno Zilberman.



**Figure 3:** Workers of *Nasutitermes* sp. licking the tergal gland of *Termitophya* sp. (Aleocharinae: Corotocini). Photo Credits: ©César Favacho.

these small beetles to become megadiverse, evolving into a highly specialized group adept at infiltrating eusocial colonies. In the context of termitophiles, certain species have developed an exceptional level of specialization towards a singular host species, giving rise to numerous lineages that rely on and are exclusively associated with specific termite species.

Currently, the subfamily Aleocharinae comprises 62 tribes, being 12 of them exclusively termitophilous: Corotocini (230 spp.), Drepanoxenini (8 spp.), Feldini (28 spp.), Philotermitini (12 spp.), Pseudoperinthini (26 spp.), Skatitoxenini (2 spp.), Termitodiscini (43 spp.), Termitohospitini (39 spp.), Termitonannini (86 spp.), Termitopaediini (81 spp.), Termitosuni (47 spp.), and Trichopseniini (50 spp.).

### **Corotocini: The most remarkable guests of termite colonies**

Across the several lineages of rove beetles which live in association with termite colonies, one of them had been exhaustively studied. The tribe Corotocini comprehends only obligatory termitophile species, and they are also reported as the "most specialized termite guests", as they present astonishing modification towards their lifestyle (Kistner, 1969; Seevers, 1957; Jacobson *et al.*, 1986). In addition, they are noteworthy for the remarkable post-imaginal growth, that results in extreme cases of physogastry (discussed in details in Chapter 2).

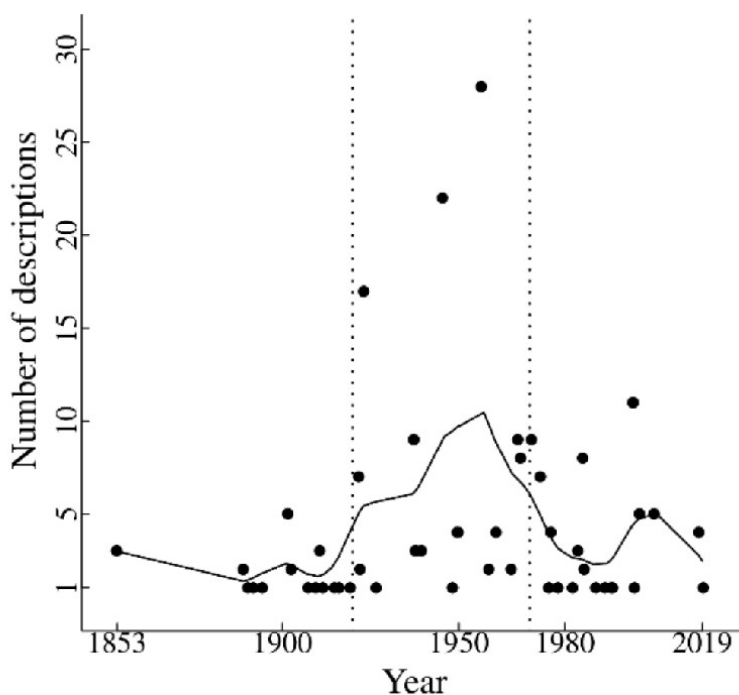
Corotocini species are widespread among all continents (except Antarctica), and the tribe encompasses 230 species grouped in 64 genera, even though recent estimates suggest that there are over 3500 undescribed species (Eloi *et al.*, 2020). Most species are host-specific, i.e, are found in association with a single termite species, the majority from the subfamily Nasutitermitinae. There are rare cases in which the same species of Corotocini is found in more than one termite host, and these cases are those in which the termite species possess a close phylogenetic affinity or are geographically isolated (Orlov *et al.*, 2021b; Pires-Silva *et al.*, 2021).

The tribe was established by Fenyes in (1918), to include termitophilous and myrmecophilous genera with a 4-4-4 tarsal formula. Soon later was reduced to a subtribe of Hygronomini (Corotocina) (Bernhauer and Scheerpeltz, 1926). Years later, Seevers (1957) returned to tribal status (Corotocini) and proposed that the group was closely related to another termitophilous tribe, Termitonannini. According to Seevers, all Corotocini species are recognizable by the four characters: 1, physogastry; 2, mentum fused to submentum; 3, mesocoxal acetabula unmarginated; and 4, terminal antennomeres with two or more coeloconic sensilla (Seevers, 1957). Years later, Jacobson *et al.* (1986) conducted a major revision of the tribe, including all the genera. The author confirmed the monophyletism of Corotocini, and the close affinity with the sister tribe Termitonannini (as previously suggested by Seevers), in addition to several infratribal groupings (Jacobson *et al.*, 1986).

Corotocini members are recognized by the following characters: tarsal formula 5-5-5 (although in some taxa 4-4-4); mentum fused to submentum; apical antennomere with one pair

of coeloconic sensilla; mesocoxal cavities free; hind coxae triangular; and the abdomen with a degree of physogastry, from moderate to strong physogastric in most species. Currently, the tribe is separated into 11 subtribes, Abrotelina, Corotocina, Eburniogastrina, Nasutitelina, Sphuridaethina, Termitoceina, Termitocupidina, Termitogastrina, Termitopithina, Termitoptochina, and Timeparthenina (Seevers, 1957; Jacobson et al., 1986; Orlov et al., 2021b).

Research on Corotocini has predominantly followed a straightforward trajectory over the last 170 years<sup>2</sup>, primarily emphasizing taxonomical descriptions (Fig. 4). Consequently, several aspects of the biology of Corotocini have remained unknown, with advancements in ecological and ethological studies emerging more prominently in the 21st century (Cunha et al., 2015; Oliveira et al., 2018; Pires-Silva et al., 2019; Zilberman et al., 2019; Pires-Silva et al., 2022).



**Figure 4:** Description rate of Corotocini across the years (1853 – 2019). Data points are the number of species described in a given year, and vertical lines delimit peak taxonomic effort (1930 to 1970s). Figure from Eloi et al. (2020), re-used with permission from the authors.

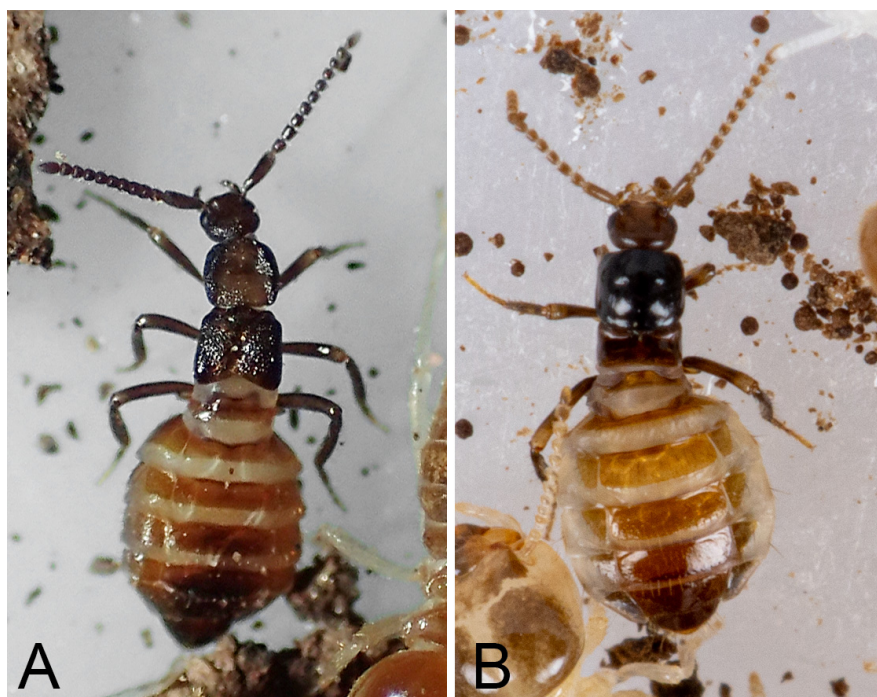
Nonetheless, older termitologists such as Renato L. Araújo and Alfred Emerson made significant contributions that greatly expanded our knowledge of the diversity of Corotocini beetles in the Neotropics. They had the habit to sample not only termites but also the guests inhabiting the nests. From part of the material from their collections, Seevers (1957) conducted a comprehensive revision of termitophilous rove beetles, shedding light on the true extent of diversity among these beetles. Despite these substantial taxonomic endeavors,

<sup>2</sup>From the period of 1853 to 2023

there remain numerous groups within Corotocini that require further attention to achieve a degree of taxonomical stability.

### The subtribe Termitogastrina Bernhauer & Scheerpeltz, 1926 and the genus *Xenogaster* Wasmann, 1891

To date, the subtribe Termitogastrina comprises 19 genera, and 82 species, all physogastric. Most species are found in the Neotropical, and Afrotropical regions. The taxonomic history of the subtribe is full of taxonomic incongruities, synonyms, and rearrangements (Seevers, 1941, 1957; Pires-Silva, 2023). Probably this is related to the fact that several species of Termitogastrina can be found together in association with a same termite species, which likely led to identification errors (Emerson, 1935; Seevers, 1957; Kistner, 2006; Pires-Silva, 2023). Moreover, the challenges associated with accurately identifying type-material, as well as the presence of ambiguous and imprecise diagnostic characters, likely arise from the small size and similarities among species within the subtribe (Fig. 5) (Zilberman, 2020; Pires-Silva, 2023).



**Figure 5:** Specimens of (A) *Xenogaster subnuda* Seevers, and (B) *Termitogaster* cf. *emersoni* Mann showing a striking morphological similarity. Photo Credits: (A) ©Tiago Carrijo, and (B) ©César Favacho.

Termitogastrina is divided into two infratribes. The infratribe Termitellici includes: *Mil-lotoca* Paulian, 1948; *Rhadinoxenus* Kistner, 1975; *Leucoptochus* Kistner, 1973; *Melanoptochus* Kistner, 1973; *Idioptochus* Seevers, 1957; *Termitellodes* Seevers, 1957; *Termitella* Wasmann,



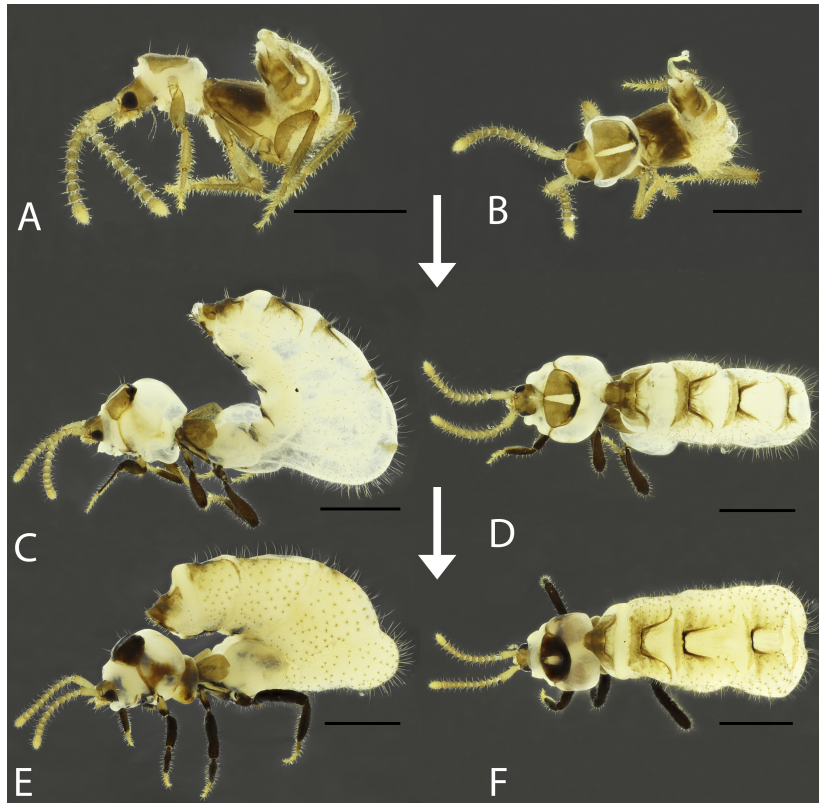
1911; *Termella* Pasteels, 1967; *Idiogaster* Wasmann, 1912. Termitogastrici encompasses: *Neotermiogaster* Seevers, 1939; *Termitogaster* Casey, 1889; *Termitosyne* Seevers, 1957; *Termitosynodes* Seevers, 1957; *Termitomorpha* Wasmann, 1894; *Xenopelta* Mann, 1923; *Termitonasus* Borgmeier, 1959; *Termitoides* Seevers, 1939; *Trachopeplus* Mann, 1923; *Xenogaster* Wasmann, 1891.

The major revision of Corotocini was conducted by [Jacobson et al. \(1986\)](#), and included all 19 genera described in Termitogastrina. The analysis recovered the “Termitogastrina” branch including only the subtribe monophyletic Termitogastrina. This branch is sustained by the 5-5-5 tarsal formula with the two last tarsomeres separated by a suture, dorsal surface of pronotum broadly impressed, and both outer and inner paratergites present and well sclerotized, with the outer paratergite considerably narrower than the inner ([Jacobson et al., 1986](#)). The two infratribes of Termitogastrina are distinguished by the shape of the glandular openings in tergite VII, and this is also related to their respective geographical distribution. The genera in the infratribe Termitellici are endemic to Africa, and all species have a single glandular opening, whereas genera in Termitogastrici have two widely separated reservoirs, and all species are restricted to the Neotropics. The number, shape, and position of glandular openings are also good interspecific characters within each infratribe (see section ??).

Many groups within Termitogastrina have remained relatively unchanged since Seevers' (1957) comprehensive work. The genus *Xenogaster* stands out as one of the most diverse within the subtribe, but since its description ([Wasmann, 1891](#)), the genus was only reviewed by Seevers in 1957. Although all species described at that time have undergone re-description, the morphological data are outdated and some new observed characters have proven valuable in providing essential information for the description and differentiation of species within Aleocharinae. This includes data related to chaetotaxy and genitalia ([Sawada, 1970, 1972](#)). Moreover, there is no deep investigation on the biological aspects of *Xenogaster*, with a plenty of anecdotal observations available for several other genera within the subtribe ([Kistner and Jacobson, 1976](#); [Kistner, 1979](#)).

In addition to their high degree of physogastry, species in Corotocini undergoes a phenomenon known as post-imaginal growth ([Kistner, 1979](#)). Upon emerging from the pupal stage, termitophiles initially resemble typical rove beetles ([Pires-Silva et al., 2019](#)). However, once they arrive at their host's nest, they undergo a significant enlargement of their thoracic, and abdominal regions ([Pires-Silva et al., 2022](#)). Within Corotocini, these transformations can be particularly extreme, involving remarkable alterations in both their body structure and behavioral patterns. This adaptation leads to remarkable modifications, including the development of pseudoappendages and the ability to undergo shapeshifting of their sclerites (Fig. 6) ([Kistner, 1982b](#); [Silva et al., 2022](#); [Pires-Silva and Zilberman, 2023](#)). Only more recently the phenomena of post-imaginal growth was highlighted in detail in Termitogastrina, with more evidences that such phenomenon is a gradual process, with predictable development, taxonomical implication, and that the body changes varies across several taxa

(Pires-Silva and Zilberman, 2023).



**Figure 6:** Post-imaginal growth development in *Thyroxenus alakazam* Pires-Silva, Zilberman & Eloi (discussed in detail in Pires-Silva et al. (2022)). The beetle emerges as an typical free-living rove beetle (A, B), and then undergoes a gradual process of expansion of thoracic and abdominal regions (C – F).

This dissertation was undertaken to address the gaps in taxonomical and biological knowledge concerning *Xenogaster*. Firstly, a cladistic analysis was conducted to elucidate the relationships among species within the genus, alongside the detailed description and redescription of all species (Chapter 1). Secondly, in the process of gathering the data for this taxonomic work, valuable information pertaining to post-imaginal growth phenomena in *Xenogaster* was also collected. These new findings enabled a thorough examination of the biology of *Xenogaster*, with a particular focus on aspects related to post-imaginal growth phenomena (Chapter 2).

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**1 | Cladistic analysis and taxonomic revision of the termitophilous genus *Xenogaster* Wasmann, 1891 (Staphylinidae, Aleocharinae, Corotocini)**

## 1.1 Introduction

About 38 years after the first record of a termitophile (Schjødte, 1853), the Austrian entomologist Erich Wasmann published in 1891 at Zoologisch-Botanische Gesellschaft the description of a new genus and species of those organisms, *Xenogaster inflata*, based on four specimens collected by the engineer Lothar Hetschko somewhere close to Blumenau in the state of Santa Catarina in Brazil. Unfortunately, the descriptive work made by Wasmann (1891) does not provide detailed information on the collection of organisms, even leaving open what their host would be. But the morphology was described in detail.

Wasmann then stated that the habitus of that “strange” (which probably led to the generic name, see section ??) animal would indicate to be an inquiline for both termites or ants, which were later identified as termites belonging to the genus *Cortaritermes* Dudley (Termitidae) (Seevers, 1957). Although at that time termite hosts were not as well studied as ants, for instance, several authors, including Wasmann, showed a degree of concern in studying these organisms not only limiting themselves to their morphological descriptions, but also addressing ecological and ethological aspects (Schjødte, 1853; Casey, 1889; Wasmann, 1891; Warren, 1920).

About *Xenogaster*, originally monotypic, Wasmann (1891) stated about the abdomen “large and strongly thickened”, as well as long and membranous, occupying about 3/4 of the total body length, comparing it to the shape of a “pear”. He also points out that the position of the abdomen is not as variable between specimens, but arranged almost vertically and not tilted forward. For this termitophilous species, he pointed 4 mm in total body length, and for the abdomen, 3 mm in length and 1 mm in width. The author also characterizes the ligula as narrow and elongated, as well as containing structures that divide the apex into several fine papillae, similar to other Aleocharinae genera such as *Ecitochara* Wasmann. In addition, some characters pointed out by the author, such as the anterior legs with five tarsomeres and the shape of the labial palpi, were highlighted because they are found in members of another similar termitophilous genus, which had already been described previously: *Termitogaster* Casey, 1889; however, Wasmann also comments that other parts of the mouthparts were totally different (Casey, 1889; Wasmann and Holmgren, 1911). Later, Wasmann and Holmgren (1911) published an identification key for *Xenogaster* including two new species – *X. nigricollis* and *X. wasmanni* – based on the material used in collected in the expedition carried out by the Danish zoologist Nils Frithiof Holmgren between 1905 and 1906 in Bolivia, and Peru (Wasmann and Holmgren, 1911).

Years later, in the major revision of termitophilous rove beetles conducted by Seevers (1957), the author noticed the presumably similarity of *Xenogaster* with *Termitogaster* (Fig. 5), and listed the some characteristics that could lead to misidentifications between the two genera, such as the morphology of the elytra and pronotum, head coloration, body length, and

general appearance (although this latter was not very useful). Wasmann (1891) had also recognized the similarities between the genera. Moreover, when analyzing material from Wasmann's collection, Seevers noticed that among the four specimens used in the description of *Xenogaster inflata* not all specimens belong to that species, and some to an undescribed one, *X. subnuda* Seevers, 1957. Unfortunately, Seevers does not inform on how many specimens of this series he based the description of that species, emphasizing only that he studied the specimens labeled "*X. inflata*" in Wasmann's collection (Seevers, 1957, pg. 102).

Due to the similarity between members of *Xenogaster* and *Termitogaster*, a number of inaccuracies and transfers surround the taxonomy of these two genera. For instance, Wasmann and Holmgren (1911) describe *X. wasmanni*, distinguishing it from *X. nigricollis* Silvestri, 1901 only by the size of second antennomere, which is larger than the third in *X. wasmanni*, being the only diagnostic character proposed. Even more conspicuous, "types" of *X. wasmanni* in Wasmann collection are not in accordance of the diagnosis provided by the author himself (Seevers, 1957). Both species were later transferred to *Termitogaster* (Seevers, 1957), but ambiguities have remained.

In a small revision of some Corotocini genera from Latin America, Kistner (2006) described a new species of *Xenogaster*, *X. lineis*, based on a dozen of specimens collected in nests of *Nasutitermes peruanus* (Holmgren, 1910). In the same work, new species from other genera of Termitogastrina, such as *Termitogaster*, and *Termitomorpha* Wasmann were also described. Kistner (2006) was aware that there is a certain degree of similarity among some genera in the subtribe, and related to *Xenogaster*, the author stated that the genus "can be easily confused with *Termitomorpha*", providing characteristics that could set apart those two genera. However, the "diagnosis" provided for *Xenogaster*, such as "the usual impressed pronotum" did not match with the described species (Kistner, 2006).

Recently, Pires-Silva (2023a) re-visited the type-material of *X. lineis*, and verified that some specimens belonged to distinct genera. The holotype of *X. lineis*, was identified as a species of *Termitogaster*, and a new combination *Termitogaster lineis* (Kistner, 2006) was proposed. The paratypes of *X. lineis*, was recognized as a *Termitomorpha*, and was described as *T. kistneri* Pires-Silva (see Appendix B for details).

As aforementioned, the taxonomical history of *Xenogaster* is very confuse and incongruous. Only more recently, species in *Xenogaster* were described with more accuracy, and a special attention to provide a concise diagnosis for the genera and species, updating the morphological data and methodologies (Pires-Silva et al., 2023; Pires-Silva and Zilberman, 2023). In order to clarify and expand the state of knowledge within *Xenogaster*, a cladistic analysis is presented to elucidate the internal relationships among species, verify the monophyly of the genus, and to guide taxonomical decisions whenever necessary. Moreover, all species in *Xenogaster* were re-visited, the genus was characterized with more robust characters, and new taxa were also described.

## 1.2 Conclusions

Upon the results of the cladistic analysis and the taxonomic investigation, the following conclusions have been reached:

- *Xenogaster* is a monophyletic group composed by 12 species;
- A new genus, *Paraxenogaster* **gen. nov.**, was designated to include *P. fossulata* **comb. nov.**;
- *Xenogaster mexicanus* was transferred to *Trachopeplus*, resulting in a new combination, *T. mexicanus* **comb. nov.**. This decision is supported in the shared morphological transformations observed between the two species, and by their association with the same host colony of *Nasutitermes nigriceps*;
- Several characters have proven to be valuable for phylogenetic relationships within the genus *Xenogaster*, as those related to chaetotaxy, mandibular pores distribution, the morphology of the glandular openings in tergite VII, and characters related to sexual dimorphism (chaetotaxy, shape of tergites, and sternites, and the presence of sclerotized apodemes in the sternite VIII of females). These distinctive traits not only contribute significantly to the taxonomic and cladistic understanding of *Xenogaster* but also offer potential utility in broader taxonomic contexts, such as within the subtribe Termitogastrina.

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**2 | Exploring post-imaginal growth phenomena in *Xenogaster* Wasmann, 1891 (Coleoptera: Staphylinidae: Corotocini)**

## 2.1 Introduction

The tribe Corotocini is recognized for being the "most specialized guests of termite nests" (Seevers, 1957; Jacobson et al., 1986). In addition to their high degree of physogastry, all Corotocini undergoes a phenomenon known as post-imaginal growth (Kistner, 1969). These beetles emerges from the pupae as ordinary rove beetles, slender and capable of flying, and after reaching the host termite colony, their bodies undergoes a gradual process of the enlargement of their abdomen and/or thorax, and secondary sclerotization (Seevers, 1957; Kistner, 1979). Species from the subtribe Corotocina, shows the most striking body changes in terms of post-imaginal growth, with the development of pseudoappendages, shape-shifting sclerites, and the growth of a recurved inflated membranous abdomen (Seevers, 1957; Pires-Silva et al., 2022). Although most authors are aware of how this phenomenon works in the majority of termitophilous species, it has been shallowly explored in others, such as in the subtribe Termitogastrina (Kistner and Jacobson, 1976).

Post-imaginal development undergoes differently by taxa, affecting different body parts into different degrees (Kistner, 1982; Pires-Silva et al., 2019, 2022; Silva et al., 2022). Seevers (1957) was probably the first to call attention to the fact that this phenomenon was receiving almost no consideration despite the hypertrophy of the abdomen. Even though, he seems to have underestimated the phenomenon in Termitogastrina to the detriment of the clearly more impressive changes that occur in Corotocina (Pires-Silva et al., 2022; Zilberman and Pires-Silva, 2023), as he states: "Apart from being considerably larger than in free-living species, the abdominal sclerites are not unusually modified in the South American genera of the subtribe, nor do extreme post-imaginal changes occur as in the Corotocina" (Seevers, 1957: 32).

Later on, Kistner and Jacobson (1976) stated that in Termitogastrina "extensive changes do occur [...] both in the abdomen as well in the sclerotized portions. This is particularly noticeable in pronotum. The stenogastric individuals have similarly shaped, but less extensively sclerotized spermathecae" (Kistner and Jacobson, 1976: 23). Moreover, regarding to the pronotum, the authors above stated that stenogastric specimens of *Termitogaster insolens* Casey present initially their pronotum deeply impressed. But later, it expands out, ending up with the ordinary convex shape. In the final stage, the pronotum is "extremely heavy and rounded" (Kistner and Jacobson, 1976: 22). The aforementioned authors did not add any further observation of other sclerotized areas; and in fact, years before, Kistner (1970) stated that for the South African *Idiogaster trinervoides* Kistner "nearly all of the post-imaginal growth [...] occurs in the membrane and that no apparent changes take place in the sclerotization or size of structure of the legs or the metasternum" (Kistner, 1970: 171).

As the post-imaginal growth occurs gradually, previous authors found that the phenomenon varies across taxa in which it is manifested (Seevers, 1957; Kistner and Jacobson,

1976; Kistner, 1979), and recently it has been accepted that this phenomenon has phylogenetical and taxonomical significance (Pires-Silva et al., 2019; Zilberman, 2020; Pires-Silva et al., 2022; Silva et al., 2022; Pires-Silva and Zilberman, 2023). The most recent hypothesis to explain how post-imaginal growth occurs in Termitogastrina was proposed by Pires-Silva and Zilberman (2023). The authors explored this phenomenon in the genus *Xenogaster*, with an unique specimen available, providing evidence that even a specimen that had not undergone all the body changes proportionate by post-imaginal growth can still be recognized, identified to specific level, and described in the case of new taxa. Pires-Silva and Zilberman (2023) discussed this phenomenon based in only one specimen of *X. lugens* Pires-Silva & Zilberman, the first stenogastric found in the genus, and compared how post-imaginal growth occurs in the *Xenogaster* based on another species, *X. pilosula* Seevers. Therefore, their work had some gaps regarding the gradual growth that occurs in the genus, but was a start for this subject related to *Xenogaster*.

However, in recent collections in Southeast Brazil, several other specimens of *X. pilosula* were collected, ranging from newly emerged stenogastric beetles to fully grown physogastric ones. In this context, I review the post-imaginal growth phenomena in *Xenogaster* recently elucidated by Pires-Silva and Zilberman (2023), providing new evidence on how this phenomenon occurs in the genus and also discussing the previous hypotheses raised by the authors.

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## General Conclusions

The genus *Xenogaster* is monophyletic, and until now, it had a disjunct distribution in South America. However, through the support of a cladistic analysis, the genus's range has now been refined, restricted to the South and Southeastern regions of Brazil. This refinement is the result of a comprehensive approach that combines morphological data, complemented by insights from the beetle's biology. This multifaceted approach has demonstrated its efficacy in making taxonomic determinations not only within the *Xenogaster* genus but also on a broader scale within the Termitogastrina subtribe. A noteworthy characteristic of these termite-associated beetles is their high degree of speciation, as they tend to coexist exclusively with a single termite species. This phenomenon not only contributes to their distinctive ecological roles but also enhances the reliability of species identification and ensures accurate taxonomic classification.

Characters related to chaetotaxy and pronotum shape have emerged as indispensable tools for the classification of species within *Xenogaster*. These characters also play a pivotal role in the description and identification of species within the framework of alpha taxonomy. For instance, species like *X. lugens* can be readily distinguished by the distinctive presence of two bristles in the medial region of tergite VII. Furthermore, the characters encompassing the number, shape, and positioning of glandular openings on tergite VII have not only proven valuable for delineating supra-specific groups but have also proved to be fundamental in elucidating the internal relationships within the Termitogastrina subtribe, to which *Xenogaster* belongs.

Furthermore, this study has amassed significant biological insights into *Xenogaster*, a taxon shrouded in gaps within the broader context of the Corotocini tribe. Of particular note is the elucidation of the post-imaginal growth phenomenon, a process shared by all species in this tribe, which has now been comprehensively documented within the *Xenogaster* genus. This documentation extends from the initial emergence of the beetle (the estenogastric stage)



through to the ultimate physogastric stage, providing a detailed account of the various developmental phases (steps). This comprehensive understanding now enables the anticipation, or predictability, of developmental changes at each stage and the ultimate morphological characteristics (i.e full grown-physogastric) of the beetle, based on its current developmental "step".

As previously emphasized, the resolution of existing uncertainties within a scientific framework holds equal importance to introducing new questions. Taxonomy should not be considered as a self-contained objective, confined to the mere act of naming organisms, but rather it should be leveraged as a powerful tool for addressing larger, supra-specific issues under the light of the evolution. This study serves as a testament to the efficacy of a holistic approach that extends beyond the realm of morphology, particularly when applied to taxa that rely on obligate associations with other species. In doing so, it significantly contributes to our enhanced comprehension of the diversity, distribution and evolution, within this captivating group of beetles.