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ORIGINAL ARTICLE / ARTÍCULO ORIGINAL

BIODIVERSITY OF PARASITES INFECTING *BOTHROPS ERYTHROMELAS* AMARAL, 1923 (SQUAMATA, VIPERIDAE): AN ENDEMIC VENOMOUS SNAKE SPECIES FROM THE BRAZILIAN NORTHEAST

BIODIVERSIDAD DE PARÁSITOS QUE INFECTAN A *BOTHROPS ERYTHROMELAS* AMARAL, 1923 (SQUAMATA, VIPERIDAE): UNA ESPECIE DE SERPIENTE VENENOSA ENDÉMICA DEL NORESTE DE BRASIL

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Running Head: Biodiversity of parasites infecting *Bothrops erythromelas*

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ABSTRACT

The knowledge of parasitic fauna in wild animals is essential for understanding the ecological conditions that determine the occurrence and prevalence of parasites in their hosts. With the exception of records of one Pentastomida (*Cephalobaena tetrapoda* Heymons, 1922) and two Nematoda (*Physaloptera* sp. And *Aspiculuris* sp.), detailed information about the helminth fauna associated with the jararaca *Bothrops erythromelas* Amaral, 1923 is lacking. This species has a wide distribution in the Caatinga, with records in marginal areas of the Cerrado and Atlantic Forest. Here, we describe the patterns of richness, abundance, and prevalence of helminths in *B. erythromelas,* a venomous snake from northeastern Brazil. The parasitized snakes were collected from six Brazilian states in the Northeast region: Bahia, Ceará, Paraíba, Pernambuco, Piauí, and Rio Grande do Norte. We examined the gastrointestinal tract of 127 specimens and found 76 individuals infected with at least one endoparasite, represented by

17 *taxa* of helminths: two Acanthocephala, three Cestoda, and 12 Nematoda. With our results, knowledge about hidden biodiversity is expanded, particularly as this is a pioneering study regarding the helminth fauna of *B. erythromelas.* We also describe the occurrence of the species *Physaloptera lutzi* Cristofaro, Guimarães & Rodrigues, 1976 and *Parapharyngodon hispidus* Ferreita *et al*., 2021 for the first time in snakes.

Keywords. Acanthocephala – Caatinga – Cestoda – Inventory – Nematoda – Parasites

RESUMEN

El conocimiento de la fauna parasitaria en animales silvestres es esencial para comprender las condiciones ecológicas que determinan la ocurrencia y prevalencia de parásitos en sus hospedadores. Con la excepción de registros de un Pentastomida (*Cephalobaena tetrapoda* Heymons, 1922) y dos Nematoda (*Physaloptera* sp. y *Aspiculuris* sp.), falta información detallada sobre la fauna de helmintos asociada con la jararaca *Bothrops erythromelas* Amaral, 1923. Esta especie tiene una amplia distribución en la Caatinga, con registros en áreas marginales del Cerrado y la Mata Atlántica. Aquí, describimos los patrones de riqueza, abundancia y prevalencia de helmintos en *B. erythromelas*, una serpiente venenosa del noreste de Brasil. Las serpientes parasitadas fueron recolectadas en seis estados brasileños de la región Nordeste: Bahia, Ceará, Paraíba, Pernambuco, Piauí y Rio Grande do Norte. Examinamos el tracto gastrointestinal de 127 especímenes y encontramos 76 individuos infectados con al menos un endoparásito, representado por 17 taxones de helmintos: dos Acanthocephala, tres Cestoda y 12 Nematoda. Con nuestros resultados, se amplía el conocimiento sobre la biodiversidad oculta, especialmente porque este es un estudio pionero sobre la fauna de helmintos de *B. erythromelas.* También describimos por primera vez la ocurrencia de las especies *Physaloptera lutzi* Cristofaro, Guimarães & Rodrigues, 1976 y *Parapharyngodon hispidus* Ferreira et al., 2021 en serpientes.

Palabras clave: Acanthocephala – Caatinga – Cestoda – Inventario – Nematoda – Parásitos

INTRODUCTION

Parasitological studies in reptiles have expanded in recent years, particularly those involving snakes (Ávila *et al.,* 2013; Kuzmin *et al.,* 2016; Mati *et al.,* 2015; Matias *et al.,* 2018; Quirino *et al.,* 2018; Oliveira *et al.,* 2020, 2023; Araújo *et al.,* 2020; Halán & Kottferová, 2021; Conga *et al.,* 2024), which can serve as definitive or intermediate hosts for various groups of parasites (Araújo *et al.,* 2020; Oliveira *et al.,* 2021; Ferreira-Silva *et al.,* 2022). Understanding the parasitic fauna of wild animals is crucial for comprehending ecological interactions of parasites and their hosts, including natural history, life cycles, and evolutionary aspects of this relationship (Silva, 2008; Matias *et al.,* 2018). Detrimental effects of parasites on host fitness include, among others, the alteration of coloration patterns and, consequently, negative impacts on reproductive success (Schall & Dearing, 1987; Dunlap & Schall, 1995; Levri, 1999).

Given the importance and biological diversity of the genus *Bothrops,* which comprises approximately 63 species worldwide (Uetz *et al.,* 2023), only 14 species of the genus have been studied in the Neotropical Region to understand their helminth fauna: *B. alternatus* Duméril, Bibron & Duméril, 1854, *B. asper* Garman, 1883, *B. atrox Linnaeus, 1758, B. barnetti* Parker, 1938*, B. cotiara* Gomes, 1913*, B. erythromelas* Amaral, 1923, *B. insularis* Amaral, 1922, *B. jararaca* Wied-Neuwied, 1824, *B. jararacussu* Lacerda, 1884*, B. lanceolatus* Bonnaterre, 1790*, B. mattogrossensis* Amaral, 1825*, B. moojeni* Hoge, 1966*, B. neuwiedi* Wagler, 1924*, B. pradoi* Hoge, 1948 (Conga *et al.,* 2024), however, these studies are essential for understanding interspecific relationships.

In this study, we present for the first time, a comprehensive analysis of the helminth fauna associated with *Bothrops erythromelas*, the Caatinga lancehead (jararaca-da-seca in Portuguese). *Bothrops erythromelas* is widely distributed in the Caatinga, throughout the Brazilian states of Alagoas, Bahia, Ceará, Maranhão, Minas Gerais, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, and Sergipe; with records in marginal areas along the Cerrado and Atlantic Forest ecotones (Campbell & Lamar, 2004; Nogueira *et al.,* 2019; Costa *et al.,* 2023). *Bothrops erythromelas* is the most important species from an epidemiological perspective, as it causes most of the life-threatening snake bites in the Brazilian semi-arid region (Lira-da-Silva *et al.,* 2009). Additionally, the species has a key ecological role, contributing to the population size equilibrium of several small vertebrates in the ecosystem (e.g., rodents, amphibians, lizards; Martins *et al.,* 2002). Currently, only three records of endoparasites were registered for *B. erythromelas*, one Pentastomida (*Cephalobaena tetrapoda* Heymons, 1922; Oliveira *et al.,* 2015) and two Nematoda (*Physaloptera* sp., Oliveira et al., 2018; *Aspiculuris* sp., Batista *et al.,* 2021). Therefore, a proper appreciation of the species interaction with parasites is crucial for understanding the occurrence and abundance patterns of endoparasites associated with this venomous snake, as well as the resulting medical and ecological implications (Jorge *et al.,* 2015).

MATERIALS AND METHODS

These parasitized snakes were sourced from four northeastern brazilian states: Bahia (N = 7), Ceará (N = 33), Paraíba (N = 3), Pernambuco (N = 11), Piauí (N = 1), and Rio Grande do Norte (N = 21). Specimens utilized in this investigation were retrieved from Biological Collections: specifically, the Herpetological Collection of the Regional University of Cariri - URCA (N = 20), the Herpetological Collection of the Semiarid - UFERSA (N = 8), the Herpetological Collection of the Federal University of Ceará - NUROF/UFC (N = 23), and the Herpetological Collection of the Federal University of Paraíba - UFPB (N = 25).

We carefully examined the presence of parasites in the gastrointestinal tract (esophagus, stomach, small and large intestines), liver, kidneys, lungs, gallbladder, and celomic cavity of the snakes under a stereomicroscope. Helminths were identified to the lowest possible taxonomic level. To achieve this, we stained Cestodes and Acanthocephala with alcoholic chloride carmine solution, and cleared with eugenol, while species of and Nematoda were cleared in lactic acid (Amato & Amato, 2010). To visualize the internal and external morphological characters of the helminths, we utilized an optical microscope. Following identification, all helminths were deposited in the Parasitological Collection of the Federal University of Ceara (UFC-P).

We calculated the parasitological parameters of abundance, richness, and prevalence following the method outlined by Bush *et al.* (1997), using the software Quantitative Parasitology 3.0 (Rózsa *et al*., 2000). Richness was determined as the total number of parasite species, while abundance represented the total count of parasite individuals found in each of the 76 specimens of *B. erythromelas.* To assess whether parasite richness is influenced by the linear measure of host size (snout-vent length: SVL), sex, and whether abundance is influenced by SVL, sex, and host maturity, we employed a Generalized Linear Model (GLM). In this analysis, predictor variables were included with interaction terms. Given that richness and abundance data are count data, we incorporated a Poisson error structure into the model. These statistical analyses were conducted using R version 4.3.1 (R *Core Team,* 2023).

Ethic aspects: The specimens used in this study were collected under the approved authorization (29613-1) conceived by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/SISBIO) from the Ministério do Meio Ambiente (MMA) of Brazil. The collecting, hold and storage were previously revised by the Ethics and Animal Welfare Committee from the Universidade Regional do Cariri (#00026/2015).

RESULTS

Out of the 127 snakes analyzed, 76 specimens were found to harbor parasites, comprising 17 helminth taxa: two Acanthocephala (cystacanths of *Centrorhynchus* sp. and Oligacanthorhynchidae gen. sp.) with a prevalence of 46.90%, three Cestoda (specimens of *Oochoristica* sp. and larvae of Plerocercoid and Cysticercoid) with a prevalence of 2.76%, and 12 Nematoda (*Brevimulticaecum* sp., Cosmocercidae gen. sp., *Hexametra boddaertii* Baird, 1860, *Oswaldocruzia* sp., *Parapharyngodon hispidus* Ferreita et al., 2021, *Physaloptera lutzi* Cristofaro, Guimarães & Rodrigues, 1976, *Physaloptera nordestina* Matias, Morais & Ávila*, 2020, Physaloptera* sp., *Physalopteroides venancioi* Lent et al. 1946, *Physocephalus* sp., *Strongyloides ophidiae* Pereira, 1929, and unidentified nematode larvae) with a prevalence of 50.34%. The overall parasite prevalence in *B. erythromelas* was 59.84%, with a mean infection intensity of 13.88 ± 7.0 (range: 1–350) (Table 1, Fig. 1).

Among the parasites found, the cystacanth of Oligacanthorhynchidae was the most abundant, with 350 individuals, followed by *Physaloptera* sp., with 239. The rarest species, with only one individual found, were *Brevimulticaecum* sp., *Oswaldocruzia* sp., and *Physocephalus* sp. Parasite richness was positively influenced by the SVL of the hosts, with no effect of sex or interaction between them (Table 2, Fig. 2). Parasite abundance was also positively influenced by SVL. Additionally, females tended to have higher parasite abundance than males, and both sexes tended to have higher abundance with increasing SVL (Table 3, Fig. 3).

DISCUSSION

Bothrops erythromelas exhibited a high prevalence of helminths (59.84%), similar to other species of snakes in the Viperidae family: *Bothrops moojeni* N = 50 (68%; Barrella & Silva, 2003) and *Crotalus durissus terrificus* Linnaeus, 1758 N = 12 (66%; Dias *et al.,* 2004), but contrasting with *Crotalus tzabcan* Klauber, 1952 N = 50 (14%; Carbajal-Márquez *et al.,* 2018). These comparative data support the idea that describing the helminths of a particular species is crucial to achieve a more complete comprehension of hidden patterns of parasite biodiversity.

The phylum Acanthocephala exhibits an indirect life cycle, engaging in trophic interactions with both invertebrates and vertebrates (Crompton & Nickol, 1985). Incidentally, snakes act as paratenic hosts for acanthocephalans (Travassos, 1917; Pizzatto & Madi, 2002; Pizzatto & Marques, 2006; Smales, 2007a; Matias *et al.,* 2018). In these cases, encysted larvae reside in the body cavity of snakes until they are ingested by the definitive host (Nickol, 1985). Typically, birds and mammals serve as definitive hosts, arthropods act as intermediate hosts, and snakes serve as paratenic hosts of the family Oligacanthorhynchidae (Schmidt, 1972; Nickol & Dunagan, 1989; Kennedy, 2006). Birds and mammals are potential predators of snakes, (Cardoso & Santos, 2012; Fraga *et al.,* 2013; Marques & Medeiros, 2018), including those of the genus *Bothrops* (Sazima, 1922; Oliveira & Santori, 1999; Martins *et al.,* 2003), Thus, we suggest that parasites may use snakes to reach their definitive hosts. Representatives of Oligacanthorhynchidae are known to infect snakes such as *Boa constrictor* Linnaeus, 1758, *Boiga dendrophila* Boie, 1827, *Bothrops jararacussu, Bothrops neuwiedi, Clelia clelia* Daudin, 1803, *Erythrolamprus aesculapii* Linnaeus,1758 *E. miliaris* Linnaeus,1758, *E. poecilogyrus* Wied-Neuwied, 1824, *Macrovipera lebetina obtusa Linnaeus, 1758, Mastigodryas bifossatus* Raddi,1820, *Micrurus corallinus* Merrem, 1820, *Philodryas olfersii* Lichtenstein, 1823, *P. patagoniensis* Girard, 1858, *Xenodon merremii* Wagler, 1824, and *X. histricus* Jan, 1863 (Travassos, 1917; Pizzatto & Madi, 2002; Pizzatto & Marques, 2006; Smales, 2007a; Smales, 2020).

Besides species of Oligacanthorhynchidae, we also found *Centrorhynchus* sp. in *B. erythromelas*, an acanthocephalan from family Centrorhynchidae. The genus *Centrorhynchus* infects birds of the Falconiformes and Strigiformes orders as definitive hosts and has invertebrates as intermediate hosts, with reptiles and amphibians serving as paratenic hosts (Torres & Puga, 1996). Cystacanths of *Centrorhynchus* have been recorded in snakes of the genera *Ahaetulla, Bothrops, Clelia, Chironius, Dipsa, Echinanthera, Imantodes, Helicops, Leptophis, Liophis, Mastigodryas, Tropidonotus,* and *Philodryas* (Travassos, 1926; Vizcaíno, 1993; Smales, 2007a; Smales, 2007b; Lamas & Lunaschi, 2009; Silva & Muller, 2012; Araújo-Filho *et al.,* 2018; Araújo *et al.,* 2020; Yudhana *et al.,* 2023; Conga *et al.,* 2024). In the present study, we only found cystacanths, suggesting that *B. erythromelas* acts as paratenic hosts, and the acanthocephalans use them to reach their definitive hosts, since Falconiformes and Strigiformes have already been reported preying on snakes (Martins *et al.,* 2003; Costa *et al.,* 2009; Cardoso & Santos, 2012). Species-level identification of the acanthocephalans was not possible due to the immature condition of the specimens (cystacanths), which have not yet developed the reproductive system that is fundamental for species identification.

For Cestoda, we identified the presence of *Oochoristica* sp. and Plerocercoid larvae and cysticercoid. Different species of snakes have been recognized as hosts of Cestoda, such as *Bothrops alternatus, B. jararaca, B. moojeni, Coluber* sp., *Corallus caninus* Linnaeus, 1758, *Erythrolamprus miliaris, Micrurus corallinus, Philodryas olfersii, Pseudoboa nigra* Duméril, Bibron & Duméril, 1854, and *Thamnophis* sp. (Silva *et al.,* 2001; Silva *et al.,* 2006; Chambrier *et al.,* 2010; Matias *et al.,* 2018; Araújo *et al.,* 2020). The genus *Oochoristica* has been reported in *Echis carinatus* Schneider, 1801, another Viperidae (Farooq *et al.,* 1983). In *B. erythromelas*, Cestoda were found only in early developmental stages, making species-level identification impossible.

We were able to identify most of the nematodes only at the Phylum level (Nematoda, 17 hosts), excepting one identification at the family level (Cosmocercidae gen. sp., 2 hosts), four at the genus level (*Brevimulticaecum* sp., *Oswaldocruzia* sp., *Physocephalus* sp., and *Physaloptera* sp.), due to the immature stage of the parasites, and six at the species level (*Hexametra boddaertii, Parapharyngodon hispidus, Physaloptera lutzi, Physaloptera nordestina, Physalopteroides venancioi,* and *Strongyloides ophidiae*). In terrestrial snakes, the richness of Nematoda tends to be higher, as observed in *Crotalus durissus terrificus* (7 spp.; Dias *et al.,* 2004) and *Crotalus mitchelli* Cope, 1861 (5 spp.; Goldberg *et al.,* 2013), and *Pseudoboa nigra* (3 spp.; Matias *et al.,* 2018). Our results corroborate this tendency, since the nematode fauna in *B. erythromelas* includes at least 12 nematode taxa, encompassing distinct species and larval stages. These results support previous studies (Brouat *et al.,* 2007), indicating that the dominance of nematodes in terrestrial snakes may be related to the habitat of their hosts.

The family Cosmocercidae is frequently reported infecting species of amphibians and reptiles (Rizvi, 2009; Ávila & Silva, 2010; Rizvi & Bursey, 2014; Bursey *et al.,* 2015; Araújo *et al.,* 2020; Draghi *et al.,* 2020). Immature individuals of *Brevimulticaecum* sp. have been reported in fish, amphibians, and reptiles (Sprent, 1979; Moravec & Kaiser, 1994; Moravec *et al.*, 1997; Vieira *et al.,* 2010; Silva *et al.,* 2018; Souza *et al.,* 2020). The genus *Oswaldocruzia* is commonly found in amphibians, although it has also been reported in reptiles, with some records for snakes (Durette-Desset *et al.,* 2006; Goldberg & Bursey, 2007; Anderson *et al.,* 2009; Campião *et al.,* 2014; Teles *et al.,* 2015; Oliveira *et al.,* 2017; Oliveira *et al.,* 2019; Flowers & Beane, 2023). *Physocephalus* uses snakes as paratenic hosts, coleopteran insects as intermediate hosts, and mammals as definitive hosts (Ryzhikov, 1952; Kirillov & Kirillova, 2021). The genus *Physocephalus* has been found in the following North American species of Viperidae: *Crotalus atrox* Baird & Girard, 1853*, C. molossus* Baird & Girard, 1853*, C. Pyrrhus* Cope 1866*, C. scutulatus* Kennicott, 1861*,* and *Sistrurus tergeminus* Say, 1823 (Goldberg *et al.,* 2001; Goldberg *et al.,* 2002; McAllister *et al.,* 2004; Goldberg *et al.,* 2013). Morphologically, it was not possible to identify *Brevimulticaecum* sp. and *Physocephalus* sp. at the species level due to the immature developmental stage of the larvae. Only female specimens were recorded for Cosmocercidae gen. sp. and *Oswaldocruzia* sp., consequently, the identification at species level was not possible because the main morphological characteristics for Cosmocercidae species identification are only present in males.

Nematodes of the genus *Physaloptera* are common in birds, amphibians, mammals, and reptiles (Ortlepp, 1922; Chabaud, 1975; Anderson *et al.,* 2009; Pereira *et al.,* 2012a; Maldonado Jr. *et al.,* 2019). Nine species of *Physaloptera* are known to occur in Brazilian reptiles, with four reported for snakes: *P. monodens Molin, 1860, P. liophis Vicente & Santos, 1974, P. obtusissima Molin, 1860,* and *P. nordestina* (Matias *et al.,* 2020). Until now, *Physaloptera lutzi* was described only in lizards (Brito *et al.,* 2014; Maia-Carneiro *et al.,* 2018), and this is the first record of the species occurring in a snake. *Bothrops erythromelas* is a generalist in terms of diet, feeding mainly on lizards, frogs, centipedes and mammals (Martins *et al.,* 2002; Silva-Soares *et al.,* 2022). Given that nematodes possess a cuticle resistant to stomach acids, we suggest that these helminths are associated with the ingestion of the host. *Physaloptera nordestina* was already described for the following northeastern Brazilian snakes: *Oxybelis aeneus* Wagler, 1824*, Xenodon merremii*, and *Pseudoboa nigra* (Matias *et al.,* 2020).

Hexametra boddaertii is a common nematode in Squamata (Ávila & Silva, 2010; Bursey & Brooks, 2011), known to infect *Bothrops* sp., *Crotalus durissus, Oxyrhopus trigeminus* Duméril, Bibron & Duméril, 1854, *Philodryas baroni* Berg, 1895, *P. patagoniensis,* and *Pseudoboa nigra* (Skrjabin, 1916; Sprent, 1978; Hartdegen & Gamble, 2002; Pinto *et al.,* 2010; Matias *et al.,* 2018). The genus *Parapharyngodon* has a close association with lizards, mainly of the genus *Tropidurus*, with only one species described for amphibians (Ávila & Silva, 2010; Anjos *et al.,* 2013; Araújo-Filho *et al.,* 2015; Ferreira *et al.,* 2021). *Parapharyngodon hispidus* was described in *Tropidurus hispidus* Spix, 1825 (Ferreira *et al.,* 2021), and the present record is the first for snakes. Since only one specimen of *B. erythromelas* was found with *P. hispidus,* we suggest that the infection is accidental, likely due to ingestion during the snake feeding.

Physalopteroides venancioi is the only species of the genus recorded in South America, found mainly in lizards and amphibians (Ávila & Silva, 2010; Campião *et al.,* 2014). We recorded *P. venancioi* in the small intestine of two snakes, suggesting that the infection occurred accidentally, as suggested for the snakes *Platyceps ventromaculatus* Gray 1834, *P. nigra*, and *P. olfersii* (Al-Moussawi, 2016; Matias *et al.,* 2018; Araújo *et al.,* 2020).

The genus *Strongyloides* parasitizes birds, mammals, amphibians, and reptiles (Graham *et al.,* 2024). In response to infection, animals may exhibit diarrhea, bronchopneumonia, alveolar hemorrhage, interstitial inflammation, altered breathing, enterocyte hyperplasia, and ulceration or squamous metaplasia of mucosal epithelium, depending on the worm life stage (Uzal *et al.,* 2016; Thamsborg *et al.,* 2017; Graham *et al.,* 2024). In reptiles, including snakes, *Strongyloides* infections cause respiratory difficulties and pneumonia (Walden *et al.,* 2020; Graham *et al.,* 2024). Five species of *Strongyloides* are documented in snakes: *S. gulae* Little, 1966*, S. serpentis* Little, 1966*, S. ophidiae, S. natricis* Navarro & Lluch, 1993, and *S. mirzai* Singh, 1954 (Graham *et al.,* 2024). *Strongyloides ophidiae* has been observed in the following Brazilian snakes: *Crotalus durissus, Erythrolamprus miliaris, Oxyrhopus guibei* Hoge & Romano, 1977, and *Philodryas olfersii* (Pereira, 1929a; Santos *et al.,* 2009; Mati & Melo, 2014; Mati *et al.,* 2015; Araújo *et al.,* 2020).

Transmission of *S. ophidiae* occurs through cutaneous or oral routes, signs of infection are visible after 7 days, and the species has a direct life cycle (Mati & Melo, 2014). This is the first record of *S. ophidiae* acting as a parasite of the species *B. erythromelas.*

The establishment of parasite populations and communities can be influenced by phylogenetic factors or host characteristics (Poulin, 2004; Kamiya *et al.,* 2014a, 2014b). In the present study, the body condition index (SVL) of the snake *B. erythromelas* was positively related to the richness and abundance of helminths. The host's body is considered the habitat of the parasite, such that a larger specimen can provide a greater area for exploration, colonization, and nutrients to endoparasites (Aho, 1990). Another relevant factor is that individuals with greater longevity experience prolonged exposure to parasitic agents (Aho, 1990; Korallo *et al.,* 2007; Pereira *et al.,* 2012b). This same pattern has been documented for other reptiles (Brito *et al.,* 2014; Araújo-Filho *et al.,* 2016; Silva-Neta & Ávila, 2018; Amorim & Ávila, 2019; Teixeira *et al.,* 2018; 2021; Silva *et al.*, 2023).

Of the 30 species of the genus *Bothrops* that occur in Brazil (Costa *et al.,* 2023), 12 (40%) species have been studied regarding their parasites (Conga *et al.,* 2024). The most studied species were: *B. jararaca* (10 studies: Pereira, 1929b; Rodrigues, 1968; Santos & Rolas, 1973; Fabio, 1979; Correa *et al.,* 1990; Vicente *et al.,* 1993; Scherer *et al.,* 1996; Grego *et al.,* 2004; Silva, 2005; Siqueira *et al.,* 2009), *B. moojeni* (7 studies: Travassos, 1926; Pereira, 1929b; Caubisens Poumarau, 1965; Sprent, 1979; Pinto *et al.,* 2012; Müller *et al.,* 2021), and *B. neuwiedi* (6 studies) (Travassos & Freitas, 1941; Ruiz & Leão, 1942; Silva *et al.,* 2001; Barrella & Silva 2003; Pinto *et al.,* 2012; Morais *et al.,* 2017; Müller *et al.,* 2021). This is the third study on the helminth fauna of *B. erythromelas.* Our findings indicate that among all helminth species found in our analysis, only *Physaloptera sp.* is not a new record for *B. erythromelas,* while the species *P. lutzi* and *P. hispidus* are described for the first time in snakes.

Thus, our results expand the knowledge of parasite hidden biodiversity, particularly as this study represents pioneering research on the helminth fauna of *B. erythromelas,* a venomous snake species endemic to the Caatinga.

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Table 1. Parasitological indices of endoparasites in *Bothrops erythromelas* (equivalent to hosts infected with at least one species of parasite). Development stage (DS), Larvae (L), Adut (A), Prevalence values (P%), number of endoparasites (NE), mean intensity of infection and standard deviation (MII ± SD), mean abundance (MA), site of infection (SI) Sto= stomach; Igi= large intestine; Smi= small intestine, Per= Peritoneum. Northeastern Brazilian state where the host was collected: Bahia (BA), Ceará (CE), Paraíba (PB), Pernambuco (PE), Piauí (PI), and Rio Grande do Norte (RN). * New record for *B. erythromelas* and ** new record for snakes.

Endoparasites	DS	P%	NE	MII±SD	MA	SI	States
Acanthocephala							
Centrorhynchus sp.*	L	13.2	56	5.6 ± 2.5	25	Per, Sto	CE, PE, RN
Oligacanthorhynchidae gen. sp.*	L	75.0	350	6.1 ± 4.0	46	Per, Sto, Igi, Smi	BA, CE, PB, PE, PI, RN
Cestoda							
Oochoristica sp.*	A	2.6	3	1.5 ± 1.5	1	Igi, Smi	BA, CE
Plerocercoid larvae*	L	1.3	2	2.0 ± 2.0	-	Per	RN
Cisticercoid larvae*	L	1.3	13	13.0 ± 13.0	-	Sto	CE
Nematoda							
Brevimulticaecum sp.*	L	1.3	1	1.0 ± 1.0	-	Per	CE
Cosmocercidae gen. sp.*	A	2.6	9	4.5 ± 4.5	7	Smi, Per	CE, RN
*Hexametra boddaertii**	A	9.2	22	3.1 ± 1.0	9	Per, Sto, Igi	CE, RN
Oswaldocruzia sp.*	A	1.3	1	1.0 ± 1.0	-	Sto	CE
*Parapharyngodon hispidus***	A	1.3	8	8.0 ± 8.0	-	Sto	CE
*Physaloptera lutzi***	A	13.2	41	4.1 ± 3.5	13	Per, Igi, Sto, Smi	CE, RN
*Physaloptera nordestina**	A	2.6	3	1.5 ± 1.5	1	Per, Sto	PE, RN
Physaloptera sp.	L	22.4	239	14.1 ± 9.0	65	Smi, Sto, Per,Igi	BA, CE, PE, RN
*Physalopteroides venancioi**	A	2.6	16	8.0 ± 8.0	6	Igi, Sto	BA, CE
Physocephalus sp.*	L	1.3	1	1.0 ± 1.0	-	Sto	PE
*Strongyloides ophidiae**	A	7.9	217	36.2 ± 30.5	80	Sto, Per, Smi,	CE, RN
Nematoda (not identified)	L	22.4	73	4.3 ± 2.0	17	Per, Smi, Igi	BA, CE, PE, RN

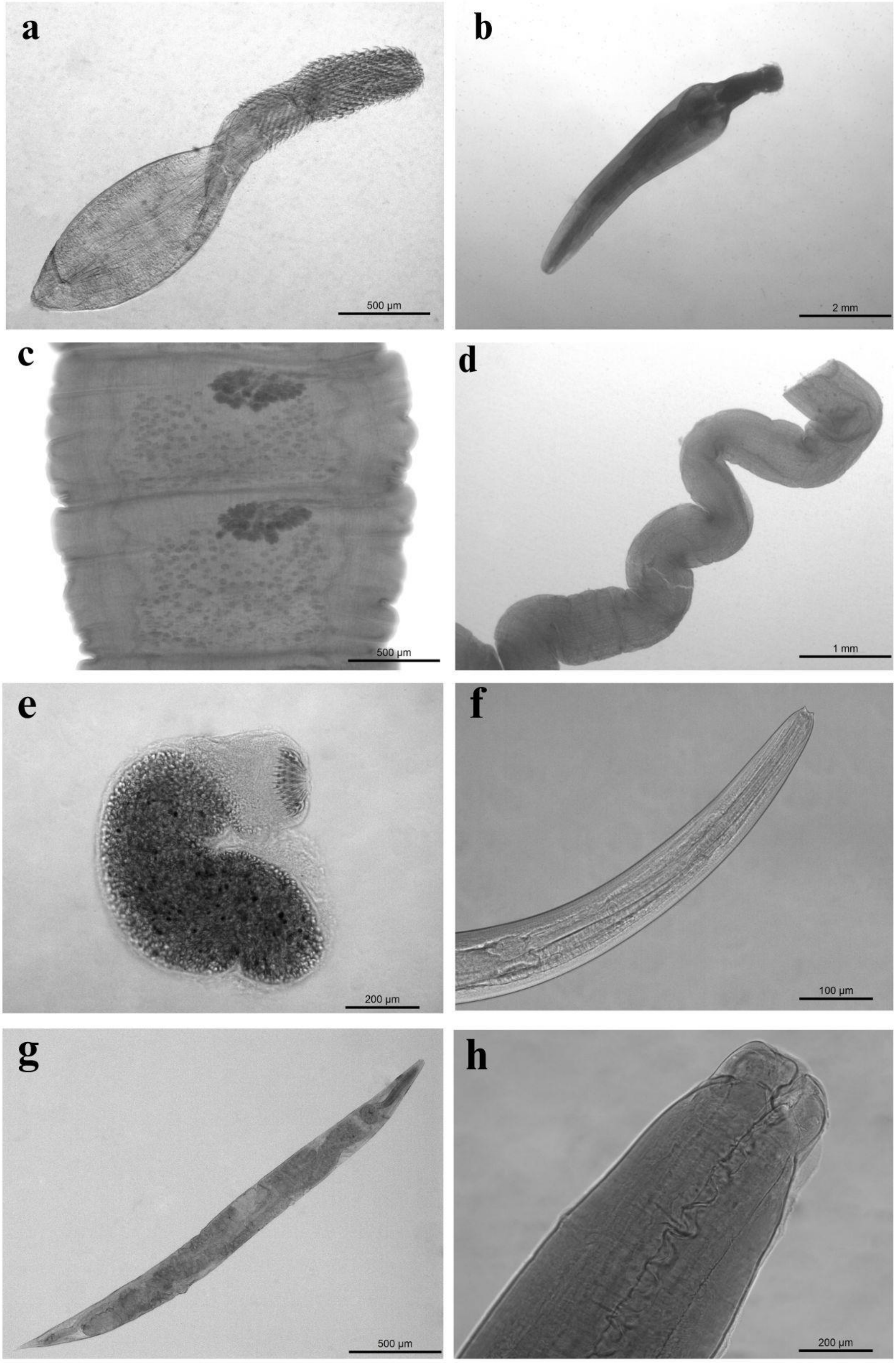
Table 2. GLM model testing how parasite richness varies as a function of host body condition index (SVL), sex, and their interactions.

Variables	Estimate	Standard error	value Z	Value P
Intercepto	-0.468	0.555	-0.844	0.398
SVL	0.003	0.001	2.188	**0.028**
Sex	0.364	1.009	0.361	0.718
SVL:Sex	-0.001	0.002	-0.446	0.655

Table 3. GLM model testing how parasite abundance varies as a function of host body condition index (SVL), sex, and their interactions.

Variables	Estimate	Standard error	Value Z	Value P
Intercept	**0.564**	**0.202**	**2.788**	**0.005**
SVL	**0.005**	**0.000**	**11.849**	**<0.001**
Sex	-0.034	0.438	-0.078	0.938
SVL: Sex	0.000	0.001	-0.255	0.798

Figure 1. Helminth species parasitizing *Bothrops erythromelas* - **Acanthocephala: a -** *Centrorhynchus* sp., **b -** Oligacanthorhynchidae gen. sp., **Cestoda: c -** *Oochoristica* sp. (mature proglottids), **d -** Plerocercoid Larvae, **e -** Cisticercoid Larvae, **Nematoda: f -** *Brevimulticaecum* sp. (anterior end of the larvae), **g -** Cosmocercidae gen. sp. (female adult), **h and I -** *Hexametra boddaertii* (anterior end and tail of the male, respectively), **j** and **k -** *Oswaldocruzia* sp. (anterior end and posterior end of the female, respectively), **l** and **m -** *Parapharyngodon hispidus* (anterior end and tail of the male, respectively), **n** and **o -** *Physaloptera lutzi* (anterior end and tail of the male, respectively) and **p -** *Physaloptera nordestina* (male's tail), **q -** *Physaloptera* sp., **r -** *Physalopteroides venancioi* (anterior end of the female), **s** and **t -** *Physocephalus* sp. (anterior end and posterior end of the larvae, respectively), **u** and **v -** *Strongyloides ophidiae* (panoramic view and eggs of the female, respectively), **w** and **x -** Nematoda not identified (anterior end and posterior end of the larvae, respectively).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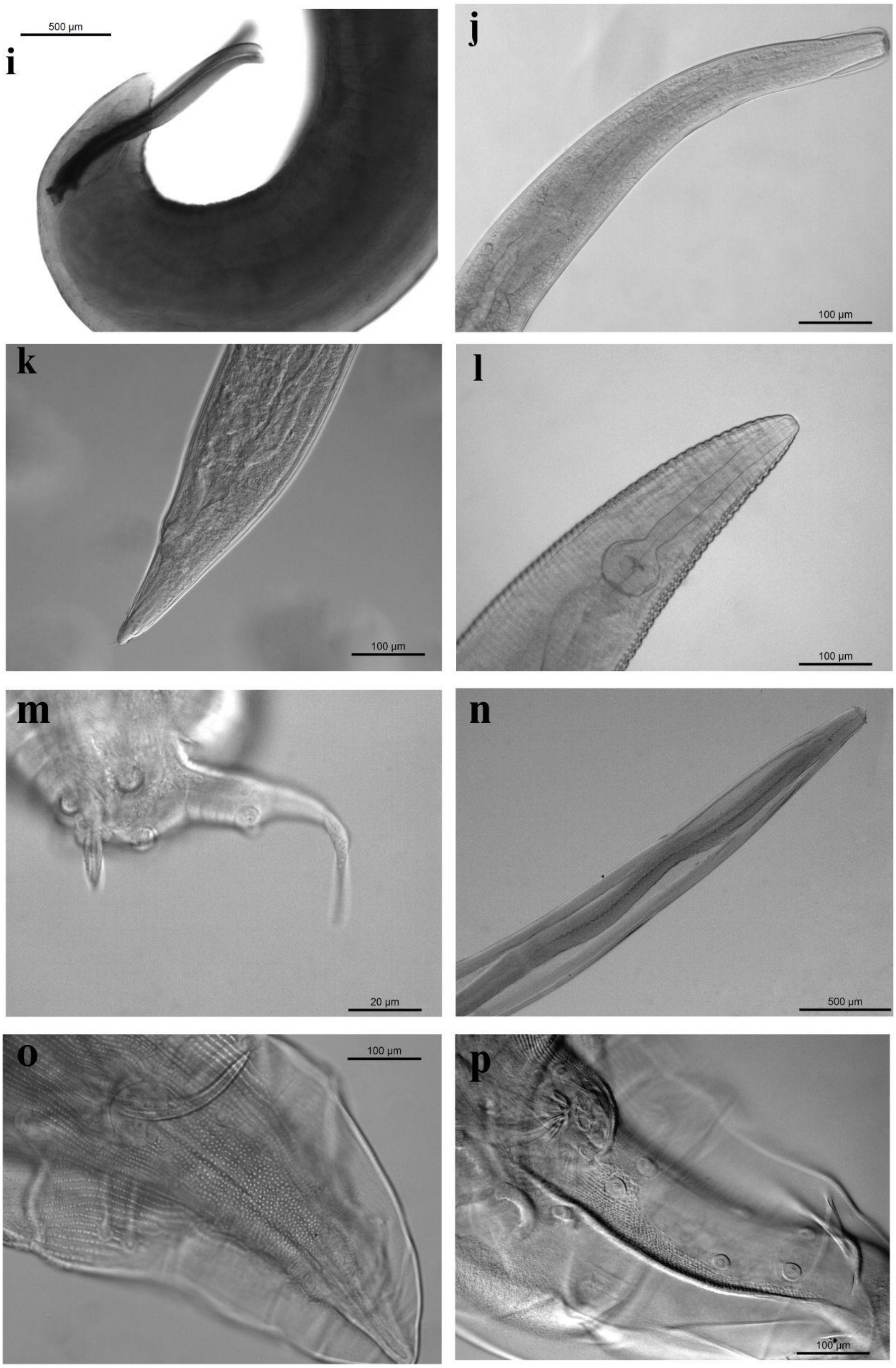
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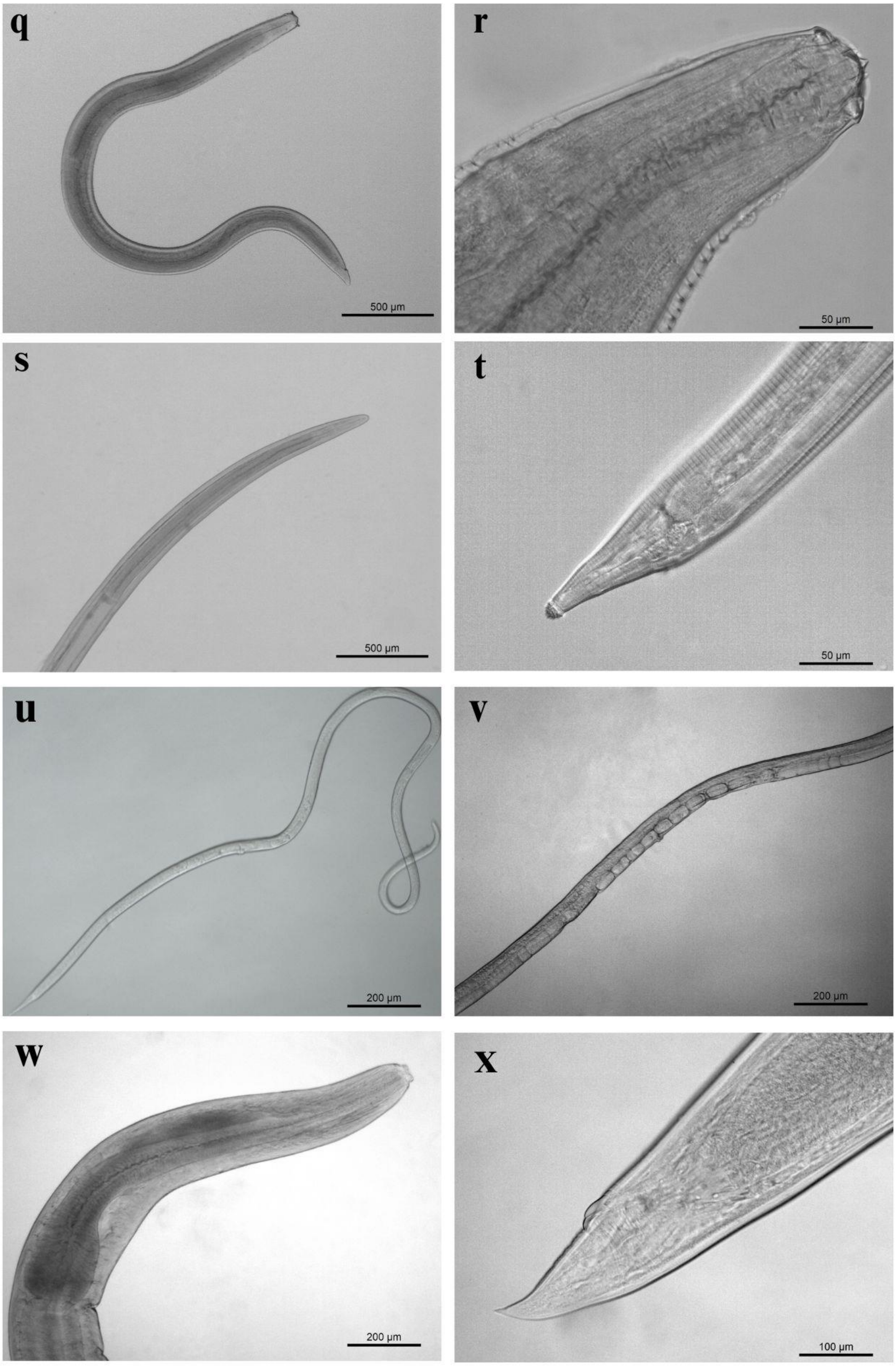
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Figure 2. Species richness of parasites in relation to the body condition index (SVL) of *B. erythromelas* specimens.

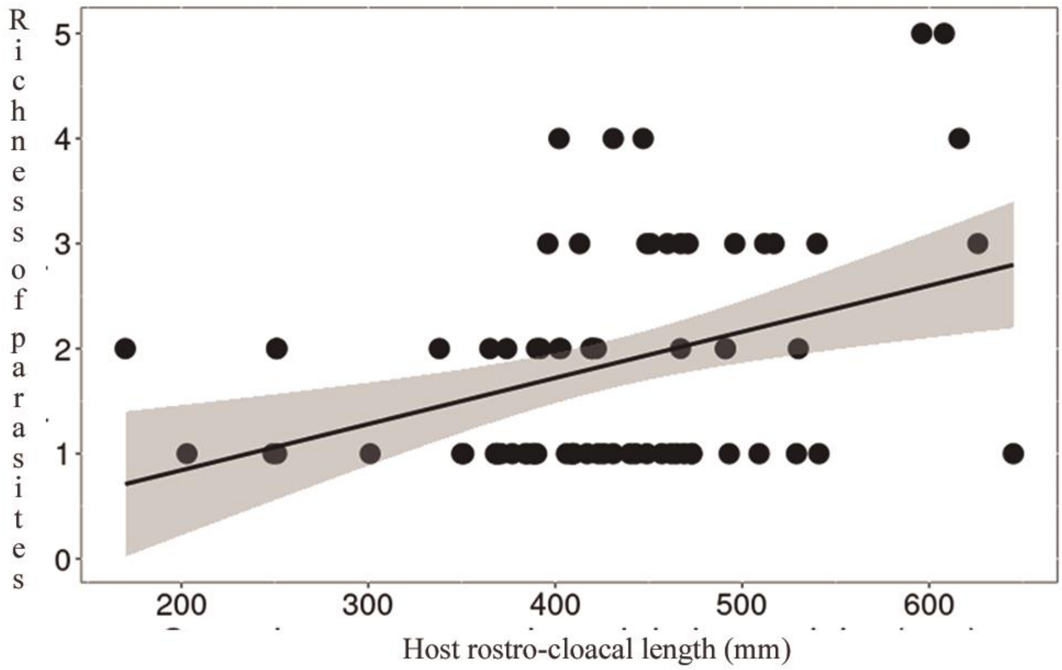

Figure 3. Parasite abundances in relation to the body condition index (SVL) for males and females of *B. erythromelas* species.