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Article

Germination of fruits eaten by the maned wolf *Chrysocyon brachyurus* (Illiger, 1815) (Carnivora, Canidae)

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Abstract: Zoochory is a fundamental process that can be the main mechanism for seed and plant dispersal for many species. Mammals of the Carnivora order are among the most important dispersing agents; however, little is known regarding the role of canids as seed dispersers. Although the maned wolf (*Chrysocyon brachyurus*) has a potentially important role in seed dispersal, given its relatively high consumption of fruits, few studies have investigated the germination rate of ingested seeds. Here, we used seeds removed from the feces of two captive specimens (maned wolf treatment) and those directly collected from unconsumed fruits (control) in germination essays to evaluate the germination rate and emergence velocity index (IVE). We used mature fruits from five species of trees in the Cerrado and Atlantic Forest in a 5 (species) × 2 (method of seed collection) factorial arrangement. The passage of seeds through the digestive tract of the maned wolf favored the germination of *Genipa americana* and *Psidium guajava,* delayed germination of *Psidium cattleianum*, and maintained the germination of *Plinia cauliflora* and *Ficus obtusifolia*. Our results revealed that germination occurred for all tested plant species consumed by the maned wolf; therefore, this canid species has high dispersal potential and can be an important ally in the restoration of the Cerrado and Atlantic Forest-Cerrado contact zone ecosystems.
Keywords: *Frugivory; germination; maned wolf; seed dispersal; zoochory.*

Germinação de frutos consumidos pelo lobo-guará *Chrysocyon brachyurus* (Illiger, 1815) (Carnivora, Canidae)

Resumo: A zoocoria é um processo fundamental para muitas espécies vegetais, podendo ser o principal mecanismo de dispersão de sementes e plantas. Os mamíferos da ordem Carnivora estão entre os agentes dispersores mais importantes, contudo, pouca atenção tem sido dada ao papel dos canídeos como dispersores de sementes. Embora o lobo-guará (*Chrysocyon brachyurus*) tenha um papel potencialmente importante na dispersão de sementes dado o seu consumo relativamente elevado de frutos, poucos estudos investigaram a taxa de germinação de sementes ingeridas. Aqui utilizamos sementes retiradas de fezes de dois exemplares em cativeiro (tratamento do lobo-guará) e diretamente retiradas de frutos não consumidos (controle) em ensaios de germinação para avaliar a taxa de germinação e o índice de velocidade de emergência (IVE). Utilizamos frutos maduros de cinco espécies de árvores que ocorrem no Cerrado e Mata Atlântica formando um arranjo fatorial de 5 (espécie) × 2 (forma de coleta de sementes). A passagem das sementes pelo trato digestivo do lobo-guará favoreceu a germinação de duas espécies, *Genipa americana* e *Psidium guajava*, atrasou a germinação de uma espécie, *Psidium cattleianum* e não afetou a germinação de duas espécies, *Plinia cauliflora* e *Ficus obtusifolia*. Com base nos nossos resultados, particularmente a descoberta de que todas as espécies vegetais testadas consumidas pelo lobo-guará germinaram, concluímos que esta espécie de canídeo tem um elevado potencial de dispersão, sendo um importante aliado na restauração de ecossistemas do Cerrado e da zona de contato entre Cerrado e Mata Atlântica.
Palavras-chave: *Frugivoria; germinação; lobo-guará; dispersão de sementes; zoocoria.*

Introduction

Seed dispersal is an important mechanism for many plant species because it allows for the transport of offspring to areas distant from the parent plant, contributing to a decreased competition for resources, reduced density-dependent seedling mortality, and increased ability to finding suitable microhabitats for the establishment and colonization of new areas (Howe & Smallwood 1982, Hämäläinen et al. 2017, Souza et al. 2021). Zoochory (dispersal by animals) is the main form of seed dispersal in tropical forests, and birds and mammals are the main dispersing agents (Bascompte & Jordano 2013). This process usually involves fruit consumption followed by regurgitation or defecation of the seeds, whereby some of the ingested seeds maintain their viability after transit through animal digestive tracts (Traveset et al. 2007).

However, passage through digestive tracts can alter parameters such as the percentage, speed, and synchronization of seed germination (Paulino-Neto et al. 2016). Thus, germination can be increased, decreased, or unaltered during passage through the digestive system due to mechanical or chemical scarification of the seed tegument, rendering it more permeable to gases and water, and the loss of germination inhibitors when the fruit pulp is removed (Traveset et al. 2007).

Species of the order Carnivora are among the most important dispersing agents (Willson 1993), because they move great distances and consume various plants (Jordano et al. 2007). However, few studies have investigated the role of canids as seed dispersers (Spennemann 2021). Canids are medium to large animals that tend to be highly mobile and have long digestion times; therefore, these mammals are equipped to transport seeds over long distances (Price et al. 2015). The maned wolf (*Chrysocyon brachyurus* Illiger 1815) is a good example of a dispersal agent, as it is the largest South American canid, has an extensive home range (Dietz 1984, Jácomo et al. 2009), and maintains an omnivorous diet composed of small mammals, birds, and fruits that varies according to the seasonal availability of resources (Rodrigues et al. 2007, Queirolo et al. 2011). The maned wolf was historically widely distributed in the grassland and Cerrado areas of central South America (Paula et al. 2018), and its geographical distribution in Brazil was limited by the Amazon Forest in the north and the Caatinga and Atlantic Forest biomes in the northeast (Queirolo et al. 2011). However, the number of maned wolf records in the Atlantic Forest biome has been increasing in the states of São Paulo, Rio de Janeiro, Minas Gerais, and Paraná, particularly in deforested, agricultural, pastural, and urban areas (Bereta et al. 2017; Muscat et al. 2021). Despite this recent expansion toward the Atlantic Forest (Xavier et al. 2017), the disorderly growth of urban centers and consequent loss and alteration of the Cerrado (Coelho et al. 2008), which is the main habitat of this species, has caused a considerable reduction in suitable environments for the maintenance of maned wolf populations (Paula et al. 2018). Therefore, the species is considered “vulnerable” in Brazil (Brasil 2022, p. 74) and “near threatened” globally (Paula & DeMatteo 2015).

The Cerrado has a great wealth of native fruit plants that are essential for wildlife sustainment, ecological balance, and environmental services (Kuhlmann & Ribeiro 2016). Seed-dispersing fauna are also fundamental for the balance of this biome because seeds influence the vegetation structure and forest dynamics and are the basis of plant diversity maintenance (Estrada & Fleming 2012, Villar et al. 2019, Lautenschlager et al. 2022). Despite its richness, approximately 50% of the original Cerrado has been converted to pastures and agricultural fields (Souza et al. 2020). Environmental laws and international commitments stipulate that Brazil should restore approximately 12 million hectares of its natural habitat, of which 5 million hectares are within the Cerrado region (Federal Decree 8.972/2017) (Schmidt et al. 2019). To meet these conditions, cost-effective, practical methods that are effective on a large scale are required (Schmidt et al. 2019). Seed-dispersing canids have the potential to assist in the ecological restoration of degraded environments, thereby perpetuating and favoring the conservation of plant species (Estrada & Fleming 2012).

Animal and vegetal material is equally represented in the feces of maned wolves, with variations according to season and location (Motta-Junior & Martins 2002, Rodrigues et al. 2007, Michalski et al. 2013). Fruits are important in the maned wolf diet, and a consistently high ingestion rate is present, even in animals from disturbed landscapes (Queirolo & Motta-Junior 2007, Massara et al. 2012, Kotviski et al. 2019). The most complex and heterogeneous agroecosystems, such as permanent preservation areas and legal reserves, provide resources for carnivores (Gheler-Costa et al. 2012) and can be used as dispersal corridors amid fragmented landscapes occupied by monocultures (De Castro & Fernandez 2004, Ferreira et al. 2018). Thus, considering the long distances traveled (Carvalho & Vasconcellos, 1995), fruit consumption by this canid can aid in the restoration of agroecosystems through the distribution of seeds over new areas, where they colonize and contribute to plant diversity in these locations.

Although studies on maned wolf diets are readily attainable (Dietz 1985, Motta-Junior et al. 1996, Aragona & Setz 2001, Motta-Junior & Martins 2002, Rodrigues et al. 2007, Massara et al. 2012, Kotviski et al. 2019), few have assessed the effectiveness of this animal species as a seed dispersal agent (Motta-Junior & Martins 2002, Santos et al. 2003, Santos et al. 2013). Motta-Junior and Martins (2002) evaluated the germination parameters of seeds from plant species consumed by maned wolves at different locations in the Cerrado, while Santos et al. (2003) and Santos et al. (2013) evaluated seed germination parameters of a single plant species, *Solanum lycocarpum* (the wolf fruit). Despite these studies, knowledge on this important topic is limited, because the effectiveness of a dispersing agent in contributing to the reproductive success of plants is determined not only by diet, but also by the germination potential of seeds after passing through the digestive tract and the spatial pattern of deposition of the defecated seeds (Schupp et al. 2010).

Based on the preceding factors, and considering a diet consisting of a high consumption of fruits, as well as a wide home-range, we investigated the potential role of the maned wolf as a seed-dispersing agent of the Cerrado and Cerrado-Atlantic forest contact zone ecosystems. Accordingly, we tested the hypothesis that the effects of seed passage through the digestive tract of the maned wolf favor germination parameters (increased percentage of germinated seeds and increased speed of germination) over those of unconsumed seeds, thus indicating the importance of this species as a seed disperser in natural habitats.

Materials and Methods

1. Study area

This study was conducted at the Ilha Solteira Wildlife Conservation Center (CCFS-ISA) (20º25’58” S, 51º20’33” W), where we provided food (fruits) and collected feces from captive maned wolves. The CCFS-ISA, as well as the sites where fruits were collected, are located in a transition zone between the Cerrado and Atlantic Forest in the northwest of São Paulo State, Brazil.

2. Choice of plant species, fruit offering, and collection of feces/seeds

To evaluate the effect of passage through the digestive tract of *C. brachyurus* on the percentage and speed of fruit seed germination, we selected plant species from the Cerrado and a semideciduous seasonal forest, which is a sub-type of the Atlantic Forest, in the northwest region of the state of São Paulo. According to Motta-Júnior and Martins (2002) and Kotviski et al. (2019), the selected species are representatives of botanical families that are part of the natural diet of the maned wolf. The following plant taxa were chosen: *Genipa americana* L. (Rubiaceae family); *Psidium guajava* L., *Psidium cattleianum* Sabine, and *Plinia cauliflora* (Mart.) Kausel (Myrtaceae family); and *Ficus obtusifolia* Kunth (Moraceae family). *Genipa americana* and *F. obtusifolia* are widely distributed throughout Brazil, and occur in several biomes, including the Cerrado (Gomes 2020, Pederneiras et al. 2020). *Psidium guajava* is a commonly found naturalized species (Proença et al. 2020), while *P. cattleianum* occurs in the Cerrado and Atlantic Forest (Proença et al. 2020) and *P. cauliflora* is located in the Atlantic Forest (Stadnik et al. 2020). These taxa have specimens on the premises of the CCFS-ISA and on the Teaching, Research, and Extension Farm of UNESP (FEPE – UNESP Ilha Solteira), where we collected fruits according to their availability throughout the year. For *G. americana, P. guajava, P. cauliflora,* and *F. obtusifolia*, fruits were collected from a single specimen to avoid variations related to individual plant genetics. This method was not feasible with *P. cattleianum*; therefore, the fruits were collected from a population of plants and homogenized to constitute the treatments.

Fruits of the selected taxa (*P. cattleianum*, *G. americana*, *P. cauliflora, P. guajava, and F. obtusifolia*) were offered separately to one female and one male maned wolf in captivity (Authorization SISBIO 72225–1, Certificate CEUA/FEIS-UNESP 13/2019, and Certificate SisGen A9A3783)*,* to avoid possible co-occurrence of seeds of different species in the feces collected. Since the wolves used in the study lived in the same enclosure, it was implausible to separate the feces by individual. The fruits were offered to the animals after 24 h of fasting. This procedure is part of the food management of carnivorous animals that the CCFS-ISA applies once a week; thus, there was no change in the feeding routine. This methodology prevented contamination of the samples by species not related to this study that were used in the daily management of the animals.

The feces were collected no more than two days after the fruit offering, considering the time for the animals to digest the food, and then packed in plastic bags and taken to the laboratory. In the laboratory, feces (maned wolf treatment) and fruit pulp (control treatment) were washed with running water over plastic sieves, and the seeds were removed with tweezers and dried in trays on absorbent paper at room temperature (~25 ºC). Only whole seeds were used for the germination tests to obtain homogeneous lots.

3. Germination trials

Seeds collected from the feces of maned wolves (maned wolf treatment) and directly from the fruits (control treatment) formed two treatments with 50 seeds for each plant species and four repetitions (2 treatments × 4 repetitions × 50 seeds × 5 plant species, totaling 200 seeds of each species per treatment, 400 seeds per plant species and of 2000 total seeds), in a 5 × 2 factorial (species × method of seed collection).

The seeds were sown in propylene boxes (internal dimensions: 12.0 × 13.5 × 28.0 cm), using sand as the substrate. Fifty seeds were sown in each box (five columns with ten seeds in each column), with four repetitions for each treatment. For all species evaluated, the seeds from the control treatments were sown together with the seeds from the maned wolf treatment. Seeds of *P. cauliflora* and *G. americana* were sown on the same day that the stools were sorted and seeds were separated; because they were recalcitrant or intermediate and thus sensitive to desiccation and storage (Panza et al. 2007, Bonjovani & Barbedo 2008, Galetti et al. 2013). Sowing of *P. guajava, P. cattleianum,* and *F. obtusifolia* occurred after drying at room temperature for a maximum of 96 h, as these are orthodox seeds that are tolerant to desiccation and storage (Medeiros & Eira 2006). After sowing, all germination boxes were stored in a greenhouse without control of environmental variables.

The treatments were monitored daily for irrigation requirements, and irrigated when necessary until they were sufficiently moist. Fungal control in the germination boxes was performed by applying a solution of the fungicide Vitavax®-Thiram diluted to 1 mL.L^{-1} of water.

For the germination evaluation, daily quantification was performed for all treatments, with germination established when the seedlings emerged from the soil surface. The germination tests began at sowing, and if new seedlings did not emerge after 30 consecutive days, the tests were terminated. Germination tests were conducted from December 2020 to April 2021 for *G. americana*, January to May 2021 for *P. cauliflora*, January to April 2021 for *P. guajava*, January to May 2021 for *P. cattleianum*, and March to June 2021 for *F. obtusifolia*. The periods for the germination tests differed among the species due to the dates of sample collection and fruit offering to the maned wolves, as well as the natural germination period of each plant species.

4. Data analysis

The germination parameters used were germination percentage and germination speed, according to Maguire (1962). The germination percentage expresses the total number of germinated seeds in relation to the total number of seeds in the treatment, and is given by the formula:

$$\%G = (\sum ni * N^{-1}) * 100.$$

Equation 1: $\sum$ni = total number of seeds germinated; N = number of seeds sampled

The speed of seedling emergence was determined by the emergence velocity index (IVE), estimated using the following formula:

$$\text{IVE} = \frac{G_1}{N_1} + \frac{(G_2 - G_1)}{N_2} + \frac{(G_3 - G_2)}{N_2} + \dots + \frac{(G_f - G_n)}{N_f}.$$

Equation 2: G_1, G_2, G_3, G_n, and G_f are the number of normal seedlings counted on the first, second, third, and remaining days, and at the last count, respectively, and N_1, N_2, N_3, N_n, and N_f are the number of days from sowing to the first, second, third, remaining, and last counts, respectively, with daily evaluations of germination. Higher IVE values indicate greater germination speeds and a stronger vigor of the batch.

The values obtained in the germination tests were compared with those of the maximum tolerance table for the germination of forest species (Mapa 2009). Differences greater than the maximum tolerance allowed between the largest and smallest mean germination from repetitions were observed for the following species in the maned wolf feces: *G. americana*, *P. cauliflora*, *P. guajava*; and in the controls: *P. guajava*, *P. cattleianum*, and *F. obtusifolia*. Thus, for each of these treatments, the repetition batch that differed from the other three (considerably higher or lower value) was replaced by the average value calculated from the other repetitions. This procedure was used because we did not have a sufficient number of seeds to repeat the experiments with all species.

Possible differences in germination rates between the control and maned wolf treatments for each fruit species were tested using the chi-squared test. Differences between emergence velocity indexes (IVE) were tested using the *t-test* for normally distributed data and the Mann–Whitney test for non-normally distributed data, after checking normality with the Kolmogorov-Smirnov test. All statistical analyses were performed using Bioestat software version 5.3 (Ayres et al. 2007), and a 5% significance level was adopted.

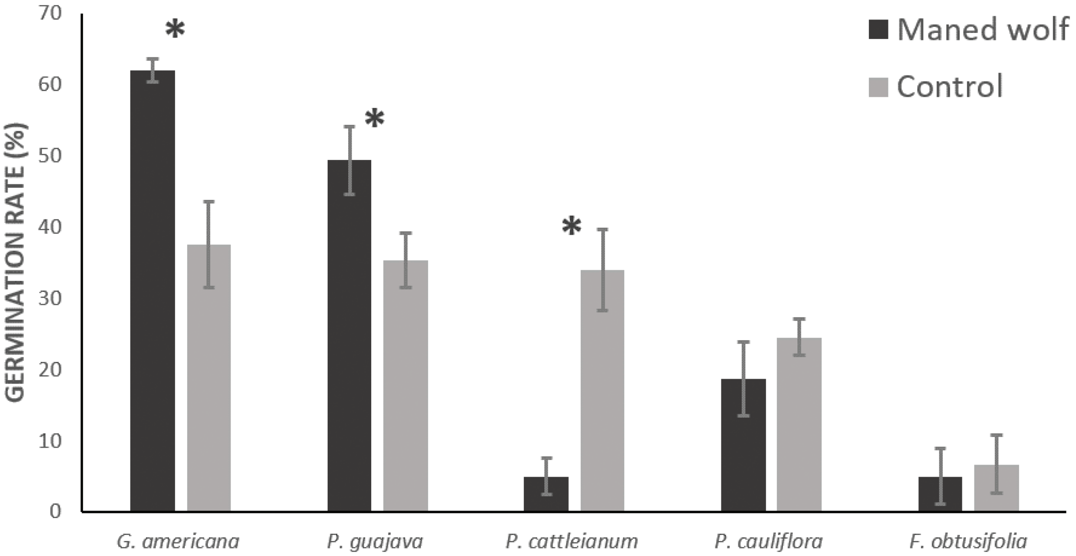

Figure 1. Germination rate (mean values and standard deviations) of seeds of *Genipa Americana, Psidium guajava, Psidium cattleianum, Plinia cauliflora* and *Ficus obtusifolia* for the maned wolf and control treatments. The (*) between columns mean statistically different values between them ($p < 0.05$).

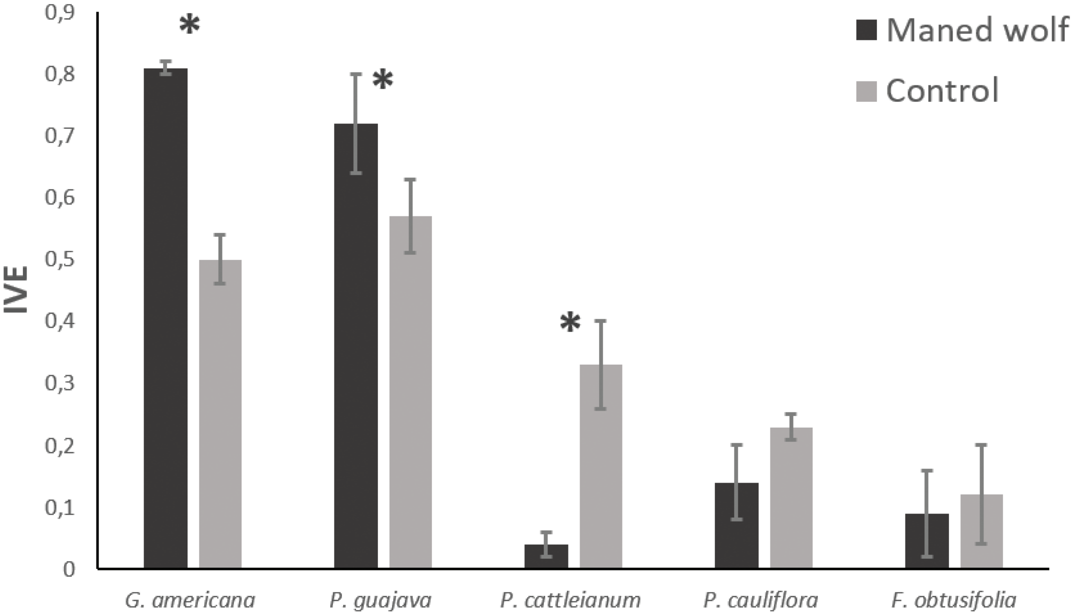

Figure 2. Emergence velocity index (IVE) (mean values and standard deviation) for seeds of *Genipa americana, Psidium guajava, Psidium cattleianum* and *Ficus obtusifolia* for the maned wolf and control treatments and for seeds of *Plinia cauliflora* (median and interquartile deviation) for the maned wolf and control treatments. The (*) between columns mean statistically different values between them ($p < 0.05$).

Results

For *G. americana* and *P. guajava* species, seeds from the maned wolf treatment showed significantly higher germination rates (%) and emergence velocity indices (IVE) than those from the control treatment (germination rates $p < 0.0001$ and $p = 0.0063$ for *G. americana* and *P. guajava,* respectively; IVE $p < 0.0001$ and $p = 0.0236$ for *G. americana* and *P. guajava,* respectively). For *P. cattleianum,* a higher germination rate (%) and emergence velocity index (IVE) were observed with the control treatment (germination rate, $p < 0.0001$; IVE, $p = 0.0001$). No significant differences were observed in seed germination rate and IVE for *P. cauliflora* and *F. obtusifolia* (germination rate $p = 0.1806$ and $p = 0.6675$ for *P. cauliflora* and *F. obtusifolia,* respectively; IVE $p = 0.1489$ and $p = 0.6026$ for *P. cauliflora* and *F. obtusifolia,* respectively) (Figures 1 and 2).

Discussion

The results obtained showed that *C. brachyurus* can act as a seed disperser in its home range, since all tested seed species germinated after consumption and defecation. Specifically, *G. americana* and *P. guajava* defecated seeds showed higher germination rates and higher velocities of seedling emergence than the controls, demonstrating a possible positive effect of the consumption of these species by maned wolves and an improvement in the germination process. These results reveal that *C. brachyurus* can both disperse the seeds and improve the propagative performance of these species.

In addition to moving within their large home range (Dietz 1984, Jácomo et al. 2009), maned wolves travel long distances daily, with an average of 14 km/night (Emmons 2012). This allows the seeds to be distanced from the mother plant, resulting in reduced plant mortality due to competition, predation, and pathogen infestation, which are common in areas with high seed densities (Janzen 1969, Cain et al. 2000). In addition, sites further away could provide improved germination and colonization of new habitats, as well as influence gene flow and the temporal and spatial genetic structure within and between populations (Willson & Travest 2000, Jordano & Godoy 2002). Furthermore, olfactory information between co-species of large canids is communicated through urine and feces that are deposited on the ground or on exposed elevated objects (Aza 2012). Maned wolves often defecate on termite mounds, anthills, and roadsides, among other structures (Dietz 1984, Aza 2012), which may play a role in increasing seed germination beyond passage through the digestive tract. For example, termite mound soils may improve water and nutrient availability to plants (Sileshi et al. 2010, Okullo & Moe 2012, Acanakwo et al. 2017) favoring germination, which is promoted by the marking habit of the species.

Although *Genipa americana* has been reported to be consumed by other canids (*Cerdocyon thous* Linnaeus 1766 and *Lycalopex vetulus* Lund 1842) in Central Brazil (Kotvisky et al. 2019), there is only one record of maned wolves feeding on this species (Bolivia; Castro & Emmons 2012), whereas species such as. *P. guajava*, *P. cauliflora*, and *Ficus* sp. have been previously identified as part of the diet of *C. brachyurus* (Motta-Junior & Martins 2002, Gressler et al. 2006, Kotviski et al. 2019). However, during the development of this study, the consumption of *G. americana* fruits was verified through necropsy of free-living specimens brought to CCFS-ISA facilities for veterinary care. This finding, along with the germination rates (62.0% for the maned wolf treatment vs. 37.5% for the control treatment) and speed of emergence indexes (0.81 vs. 0.50 for the maned wolf and control treatments, respectively) observed in this study, may indicate a mutualistic interaction between these species.

Previous reports have identified *P. guajava* as a food source for *C. brachyurus* (Motta-Junior & Martins 2002), which is one of the main species of carnivorous mammals that disperse seeds from this plant species (Gressler et al. 2006). Therefore, considering the germination rates (49.33% maned wolf treatment vs. 35.33% control treatment) and emergence velocity indexes (0.72 maned wolf treatment vs. 0.57 control treatment) observed in this study, an important mutualistic interaction may also exist between these two species, as was observed with *C. brachyurus* and *G. americana.* In a previous study, Motta-Junior & Martins (2002) observed higher germination rates for seeds of *P. guajava* (97% maned wolf treatment vs. 95% control treatment) than those observed in our study (49.33% maned wolf treatment vs. 35.33% control treatment). However, those authors found no significant differences between the treatments. In this study, we observed differences in germination parameters between *P. guajava* seeds defecated by the maned wolf and those that were unconsumed, with greater values recorded with the former treatment. These differences may be associated with methodological differences of the studies, ranging from the use of a greenhouse without control of environmental variables using sand as a substrate (this study), to experiments conducted in the laboratory with controlled light and temperature on moist filter paper (Motta-Junior & Martins 2002), or possible differences in seed quality depending on their production location.

Although *P. guajava* is a naturalized plant (Sobral et al. 2015), and its evolutionary history and domestication process are unknown (Arévalo-Marín et al. 2021), this species is highly utilized by wild animals (Gressler et al. 2006, Torres & Guitiérrez 2018), and zoochory is the main dispersal method for its seeds (Gressler et al. 2006). Non-native species have been shown to cause loss of biological diversity (Pimm et al. 1995, Sala et al. 2000); however, they can also provide conservation benefits (Schlaepfer et al. 2011), such as habitat or food resources for native species, replacements for extinct taxa, additional ecosystem services, and restoration inducements (Schlaepfer et al. 2011). Studies have shown the positive effects of *P. guajava* on forest regeneration and restoration of native tree species in tropical and subtropical forests (Aide et al. 2000, Lugo 2004, Berens et al. 2008).

Seeds of *Psidium cattleianum* are dispersed by birds, ants, bats, monkeys, and ungulates (Gressler et al. 2006). Our results indicated a delay in the germination process after passage through the digestive tract of *C. brachyurus,* which partially refuted our initial hypothesis. Unlike the results observed for the other species of fruits analyzed in this study, the physical passage of *P. cattleianum* seeds through the digestive tract of the maned wolf may have affected the viability of part of the defecated seeds, while other portions of the ingested and dispersed seeds remained viable. Increased germination speed can favor plant establishment under adverse conditions (Fenner 1985), which can be beneficial when vegetation is sparse. Delayed germination also improves diversity by allowing less competitive species to develop (Grubb 1977, Fenner 1985). The behavior of *P. cattleianum* in areas where it occurs naturally is unclear because there is a gap in the scientific literature on the ecology and behavior of this species; however, germination in the maned wolf treatment indicates that this canid may play an important role in maintaining the biodiversity of plant species through the dispersal of seeds.

Zoochory is the main dispersal method of *P. cauliflora* (Gressler et al. 2006). Gressler et al. (2006) listed the maned wolf as one of the main species of carnivorous mammals that disperse the seeds of this plant. *Ficus* sp. has also been reported as food for *C. brachyurus* (Kotviski et al. 2019) and other canids, such as *Cerdocyon thous*, *Lycalopex vetulus,* and *Canis latrans* Say 1823 (Facure et al. 2003, Silverstein 2005, Kotviski et al. 2019). Although the consumption of *P. cauliflora* and *F. obtusifolia* fruits by maned wolves has been reported, germination of the seeds was not assessed. Our study found no differences in the germination rate and speed of seedling emergence between treatments. These facts suggest that seeds of these species are not modified as they pass through the digestive system of the animal, thereby maintaining their viability for germination after consumption and dispersal by *C. brachyurus.*

Overall, our results showed that *C. brachyurus* is a canid that can act as a seed dispersal agent, since germination occurred with the maned wolf treatment for all plant taxa evaluated. This demonstrates an important mutualistic interaction between the maned wolf and these plants. Considering that greater than 90% of tropical plant species depend on animals for the dispersal of their seeds (Jordano 2000), the decrease in population and/or extinction of these conveyors (such as *C. brachyurus*, which is an endangered species) may affect partner plants and microbiome associations (Del-Claro & Dirzo 2021).

This population reduction or elimination of frugivorous animals and seed dispersers, such as *C. brachyurus*, can delay forest regeneration (Farwig & Berens 2012) and induce other negative environmental effects. For example, the disappearance of large animals has caused a reduction in the seed size of some fruit plants that are normally included in the diets of these species (Emer et al. 2020, Del-Claro & Dirzo 2021). Therefore, it is clear that seed dispersing animals are important for the conservation of the environment, and the loss of these species can have negative effects on the ecological and evolutionary dynamics of communities and compromise the processes of ecological succession and restoration of degraded areas (Fleming & Kress 2011, Rocha et al. 2012, Galetti & Dirzo 2013).

Additionally, the germination percentages and speeds reported in our results, along with the extensive home range of *C. brachyurus,* demonstrate the potential contribution of this species to the expansion of geographic dispersal, gene flow, and recruitment of the respective plants. However, there is a gap in the scientific literature in terms of ecological data and the spatial behavior of maned wolves (Aximoff et al. 2020). The species has been detected in buffer zones that contain crops such as sugarcane, soybeans, corn, and cotton, as well as silviculture and pasture areas (Santos et al. 2003, Coelho et al. 2008, Vynne et al. 2011, Vynne et al. 2014, Paolino et al. 2016, Pônzio et al. 2022). The maned wolf may travel these matrices and spread seeds across the various landscapes, contributing to the recovery of degraded areas of the Cerrado, and such forest species are commonly recommended and used in the recovery of these areas (Valeri et al. 2003, Martins et al. 2014, Nascimento et al. 2019). Furthermore, *C. brachyurus* can disperse seeds of plants that have a wide distribution, including those that occur in areas of contact between the Cerrado and the Atlantic Forest. The maned wolf has expanded into areas of this biome (Bereta et al. 2017; Muscat et al. 2021) to consume the available fruits (Motta-Júnior & Martins 2002, Kotviski et al. 2019); therefore, this species may contribute to the natural regeneration of degraded areas once covered by the Atlantic Forest. Thus, actions that contemplate the conservation of *C. brachyurus,* and consequently its ecological and functional role as a seed disperser, can assist in the implementation of management practices aimed at the maintenance or recovery of important ecological processes, including those in landscapes with anthropogenic modifications.

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Igor Paiva Ramos: Substantial contribution in the concept and design of the study; contribution to data analysis and interpretation; contribution to critical revision, adding intellectual content.

Marco Eustáquio de Sá: Substantial contribution to design of the study; contribution to critical revision, adding intellectual content.

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Conflicts of Interest

The authors declare that they have no conflicts of interest related to the publication of this manuscript.

Data Availability

Supporting data are available at <https://data.scielo.org/dataset.xhtml?persistentId=doi%3A10.48331%2Fscielodata.AQYC2S&showIngestSuccess=true&version=DRAFT>

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Short Communication

Length-weight relationships of 24 stream-dwelling fish species from the Atlantic Forest in Rio de Janeiro, Brazil

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Abstract: The length-weight relationship parameter is important for obtaining fish weight and biomass data with relevant implications about species role on ecosystem functioning. Here we report the length-weight relationship (LWR) for 24 fish species from three streams located in the Atlantic Forest in the Rio de Janeiro State, Brazil. Fish were collected with electrofishing and standard length (cm) and wet weight (g) were measured to obtain the a and b parameters of the Log (W) = Log (a) + b Log (SL) equation. Length-weight relationships for seven out of 24 species (*Hypostomus punctatus, Deuterodon taeniatus, Deuterodon hastatus, Deutorodon janeiroensis, Characidium vidali, Characidium interruptum* and *Rineloricaria zawadiskii*) are reported for the first time. The length-weight relationships reported here contribute to the database that can support fish diversity conservation, fisheries management plans and studies on fish biology.

Keywords: *biodiversity; conservation; freshwater fish.*

Relação peso-comprimento de 24 espécies de peixes de riachos da Mata Atlântica do Rio de Janeiro, Brasil

Resumo: A relação peso-comprimento é um parâmetro importante para se obter o peso do peixe e sua biomassa, fornecendo dados importantes a serem incorporados em estudos sobre o papel das espécies em processos ecossistêmicos. Aqui, reportamos as relações peso-comprimento de 24 espécies de peixes de três rios localizados na Mata Atlântica do estado do Rio de Janeiro, Brasil. Os peixes foram coletados com a pesca elétrica e seu comprimento padrão (cm) e peso (g) foram medidos para obter os parâmetros a e b da equação Log(P) = Log (a) + b Log (CP). As relações peso-comprimento de sete entre as 24 espécies (*Hypostomus punctatus, Deuterodon taeniatus, Deuterodon hastatus, Deutorodon janeiroensis, Characidium vidali, Characidium interruptum* e *Rineloricaria zawadiskii*) são reportados pela primeira vez. As relações peso-comprimento informadas contribuem para a base de dados que auxilia na conservação da diversidade de peixes, na preparação de planos de manejo de pesca e estudos da biologia de peixes.

Palavras-chave: *biodiversidade; conservação; peixes de água doce.*

Introduction

Length-weight relationships (LWR) are very important for ecological, ichthyological and fisheries studies as it allows one to calculate weight by measuring length and to estimate the condition factor, providing important information on fish physiology (Le Cren 1951, Froese 2006). Data about LWR can also elucidate different aspects about fish health, individual growth and, once the fish weight is known, it is possible to estimate the biomass of an entire population or community and thus investigate ecosystem processes and how fish species can affect them (Froese 2006, Giarrizzo et al. 2006, Joyeux et al. 2009, Camara et al. 2011, Zandonà et al. 2021, Lima et al. 2022).

Here, we report the length-weight relationships for 24 stream-dwelling fish species from three Atlantic Forest streams located in the state of Rio de Janeiro, Brazil. These fish species are relatively common in the Atlantic Forest streams, but information on length-weight relationships are missing for seven species (*Hypostomus punctatus, Deuterodon taeniatus, Deuterodon hastatus, Deuterodon janeiroensis, Characidium vidali, Characidium interruptum* and *Rineloricaria zawadiskii*) in FishBase (Froese & Pauly 2023) or other published literature. As a matter of fact, *Rineloricaria zawadiskii* was described for the first time in 2022, therefore this is the first data on LWR for this species (Silva et al. 2022). In this sense, our results can be of great importance for all researchers working in this biome.

Material and Methods

Fish were collected in three Atlantic Forest streams in Rio de Janeiro, Brazil: Rio Guapiaçu (22°26′08.2″S and 42°45′31.8″W), Rio Ubatiba (22°52′15.9″S and 42°44′14.1) and Rio Mato Grosso (22°52’24.7”S and 42°39’06.4”W) (Figure 1). Rio Guapiaçu is within the Guapiaçu-Macacu basin, which provides water to 2.5 million people among five cities in the surrounding area. Rio Guapiaçu is a fourth-order stream with a maximum width of 13m and a maximum depth of 1.5m (Manna et al. 2019). The riparian area is densely forested and the substrate composed of a mixture of bedrock, sand and leaf litter distributed across runs and pools (Manna et al. 2017). Rio Ubatiba is a low-elevation second-order stream in the Serra do Mar mountain

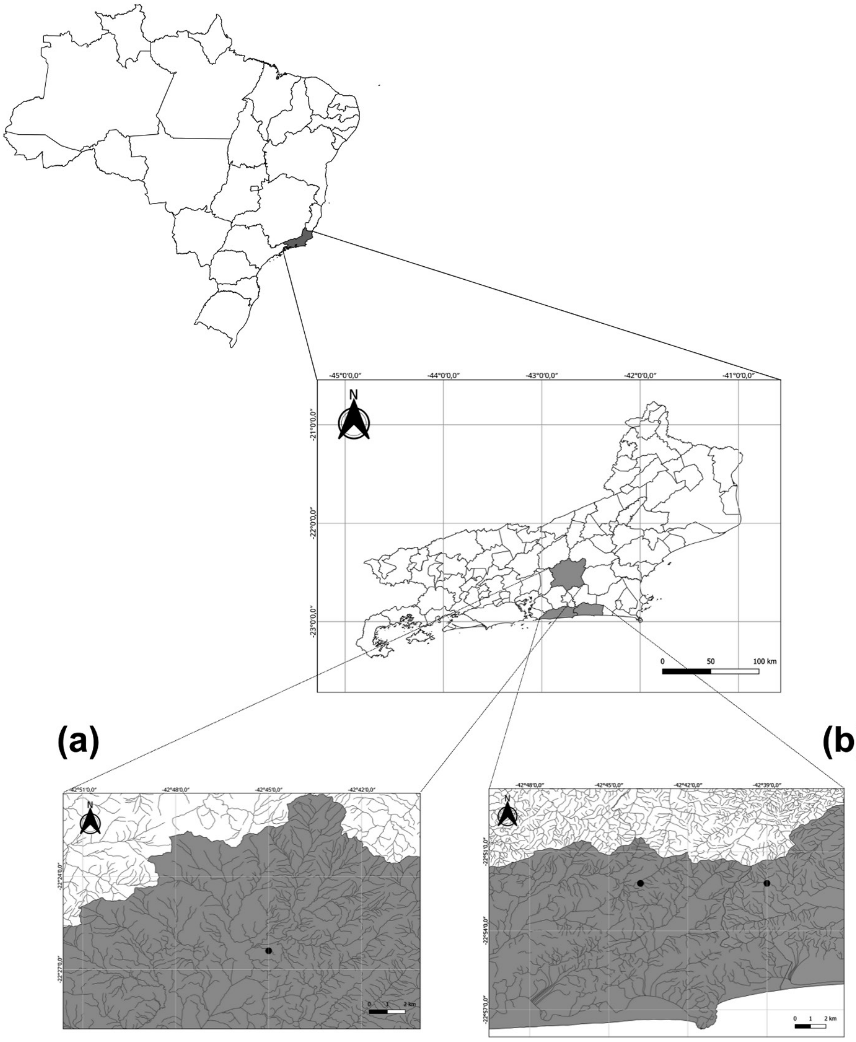

Figure 1. Map of the study area in the state of Rio de Janeiro, southeastern Brazil. Black dots = sampling sites: (a) Guapiaçu stream, municipality of Guapimirim, (b) Ubatiba and Mato Grosso streams, municipality of Maricá and Saquarema, respectively.

range. It flows through meadows deforested for agricultural practices and cattle ranching, but patches of secondary Atlantic Forest are still common on the top of the surrounding hills. The average width and depth of our sampling sites was 1.2 m and 0.4 m, respectively. Rio Mato Grosso is a third-order stream that flows for about 11 km before discharging into the Saquarema lagoon, a large brackishwater lagoon formed by the accumulation of sand dunes offshore. Average width and depth of our sampling sites was 3.6 m and 27.4 cm, respectively (this sampling site is described in more detail in Mazzoni & Lobón-Cervià 2000, Rezende et al. 2013, Manna et al. 2020).

Fish sampling was conducted in Rio Guapiaçu during the dry season in June, July, and October 2012; in Rio Ubatiba during three periods: (i) from July 1994 to July 1995, (ii) July 2015 to January 2016, and (iii) February 2019; and in Rio Mato Grosso from March 2016 to January 2017. In all sites, fish were collected in a 200-m long reach, delimited by two seine nets (mesh size 5 mm). We used a backpack portable electrofishing device (Mazzoni et al. 2000) to catch fish using successive removals (Zippin 1958). The fish were euthanized with a solution of 0.4 ml of eugenol, 3.6 ml of methanol and 1L of distilled water, and subsequently fixed in formalin 10%. After seven days, all fish specimens were preserved in 70% ethanol.

Fish species identification was confirmed by specialists at the National Museum of the Federal University of Rio de Janeiro (MN-UFRJ). After fixation, fish were measured with a caliper for standard length (to the nearest 0.01 cm) and weighted (wet weight, nearest 0.01g). The length-weight relationships were obtained using the equation Log (W) = Log (a) + b Log (SL) where W is the fish wet weight (g), and SL is the standard length (cm). The coefficient of determination (R^2) and the 95% confidence interval of the a and b parameters of the equation were calculated. Outliers were excluded by visual detection when plotting the Log W – Log SL relationship.

Results

In this study, we sampled a total of 1081 specimens belonging to 24 fish species and 11 families to obtain their length (cm) and weight (g) measurements. Length-weight relationships (LWR) from each species and study site, sample sizes (N), ranges for standard length and weight, the means and 95% Confidence Interval (95% CI) for the equation parameters a and b, and the coefficient of determination (R^2) are presented in Table 1. The coefficient of determination (R^2) ranged from 0.720 to 0.994, a values ranged from 0.0008 to 0.039 and b values from 2.55 to 3.60.

Table 1. Length-weight relationships (LWR) for 24 fish species from Atlantic Forest streams in Brazil.

Species/Family	N	Standard Length (Min-Max) (cm)	Weight (Min-Max) (g)	*a* (95% CI)	*b* (95%CI)	R^2
Rio Guapiaçu						
Characidae						
Deuterodon taeniatus	17	6.71–10.69	8.74–35.85	*0.031 (0.015–0.067)*	*2.95 (2.60–3.30*	0.956
Bryconamericus ornaticeps	23	3.44–5.07	0.82–3.00	*0.018 (0.011–0.030)*	*3.09 (2.76–3.42)*	0.948
Mimagoniates microlepis	44	1.36–4.80	0.04-2.10	*0.016 (0.014–0.017)*	*3.07 (2.98–3.16)*	0.991
Heptapteridae						
Acentronichtys leptos	19	2.86–7.74	0.156–3.761	*0.009 (0.006–0.013)*	*2.85 (2.63–3.07)*	0.977
Pimelodella lateristriga	29	2.7–10.7	0.3–14.1	*0.013 (0.010–0.017)*	*2.93 (2.80–3.07)*	0.987
Crenuchidae						
Characidium vidali	43	2.42–6.22	0.32–3.75	*0.029 (0.022–0.0038)*	*2.66 (2.48–2.84)*	0.956
Poeciliidae						
Phalloceros harpagos	18	1.53–2.77	0.10–0.47	*0.031 (0.024–0.040)*	*2.55 (2.17–2.94)*	0.924
Loricariidae						
Rineloricaria zawadiskii	24	6.14–14.70	1.55–35.0	*0.002 (0.001–0.003)*	*3.60 (3.41–3.79)*	0.986
Ancistrus multispinis	9	2.76–7.85	0.56–18.68	*0.02 (0.012–0.032)*	*3.28 (2.98–3.57)*	0.990
Callichthyidae						
Scleromystax barbatus	20	2.44–6.54	0.47–7.79	*0.039 (0.032–0.046)*	*2.82 (2.71–2.93)*	0.994
Synbranchidae						
Synbranchus marmoratus	5	21.05–34.06	9.01–41.82	*0.001 (0.000–0.025)*	*3.05 (2.03–4.07)*	0.968
Trichomycteridae						
Trichomycterus gr. *zonatus*	8	2.75–5.48	0.28–2.03	*0.016 (0.011–0.021)*	*2.83 (2.61–3.05)*	0.994

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Species/Family	N	Standard Length (Min-Max) (cm)	Weight (Min-Max) (g)	*a* (95% CI)	*b* (95%CI)	R^2
Rio Ubatiba						
Anablepidae						
Jenynsia multidentata	17	2.0–2.9	0.17–0.54	*0.019 (0.013–0.028)*	*3.19 (2.74–3.64)*	0.938
Characidae						
Deuterodon hastatus	399	2.5–6.2	0.22–8.32	*0.019 (0.016–0.022)*	*3.21 (3.11–3.31)*	0.911
Deuterodon janeiroensis	328	0.29–42.2	2.3–11.4	*0.026 (0.024–0.029)*	*3.00 (2.94–3.05*	0.973
Mimagoniates microlepis	374	1.2–4.6	0.06–1.60	*0.028 (0.025–0.032)*	*2.57 (2.44–2.69)*	0.806
Cichlidae						
Geophagus brasiliensis	115	1.0–7	0.01–16.09	*0.019 (0.017–0.021)*	*3.38 (3.31–3.46)*	0.985
Crenuchidae						
Characidium sp	154	2.6–7.2	0.2–6.48	*0.014 (0.010–0.019)*	*3.06 (2.87–3.25)*	0.864
Characidium interruptum	15	2.1–4.0	0.14–1.5	*0.015 (0.005–0.045)*	*3.09 (2.14–4.04)*	0.791
Erythrinidae						
Hoplias malabaricus	18	1.8–17.8	0.08–79.48	*0.017 (0.010–0.029)*	*2.92 (2.69–3.14)*	0.979
Heptapteridae						
Pimelodella lateristriga	94	3.7–7.4	0.61–4.99	*0.013 (0.010–0.016)*	*2.91 (2.77–3.05)*	0.949
Rhamdia quelen	12	6.4–8.3	1.99–6.03	*0.002 (0.0005–0.0074)*	*3.74 (3.09–4.39)*	0.943
Poeciliidae						
Phalloceros harpagos	90	1.0–3.2	0.02–0.69	*0.016 (0.014–0.018)*	*3.06 (2.91–3.22)*	0.946
Poecilia reticulata	13	1.4–3.3	0.04–0.68	*0.018 (0.014–0.023)*	*3.10 (2.72–3.48)*	0.966
Poecilia vivipara	98	1.0–4.0	0.01–2.13	*0.019 (0.017–0.020)*	*3.36 (3.29–3.44)*	0.987
Synbranchidae						
Synbranchus marmoratus	7	15.5–22.5	3.64–11.4	*0.0008 (0.0001–0.0005)*	*3.05 (2.44–3.65)*	0.971
Rio Mato Grosso						
Heptapteridae						
Pimelodella lateristriga	206	3.0–11.7	0.5–19.5	*0.015 (0.014–0.017)*	*2.89 (2.82–2.96)*	0.972
Rhamdia quelen	14	9.54–16.5	12.48–69.54	*0.013 (0.005–0.036)*	*3.04 (2.66–3.42)*	0.961
Loricariidae						
Hypostomus punctatus	34	2.2–11.1	0.23–25.83	*0.025 (0.017–0.037)*	*2.89 (2.58–3.20)*	0.919
Parotocinclus maculicauda	121	2.4–3.9	0.29–1.30	*0.032 (0.022–0.047)*	*2.62 (2.29–2.94)*	0.720

Discussion

In this study, we present length-weight relationships (LWR) of 24 fish species, of which seven have no previous LWR documented in FishBase (Froese & Pauly 2023). The coefficient of allometry (b) ranged from 2.55 (*Phalloceros harpagos*) to 3.74 (*Rhamdia quelen*), with the majority of the species presenting values within the expected range of 2.5–3.5 (Froese 2006).

Among the species for which LWR are reported, for *B. ornaticeps, A. leptos, P. lateristriga, S. marmoratus, T. zonatus, H. malabaricus, P. reticulata* and *R. quelen* the b value is similar to the records in FishBase (Froese & Pauly 2023). On the other hand, for *P. harpagos, S. barbatus, H. malabaricus, M. microlepis, Jenynsia multidentata* and *P. maculicauda,* b values are lower than Fishbase data, while for *A. multispinis, Poecilia vivipara* and *G. brasiliensis,* b values are higher. This variability in b values is also present in previous studies and can be due to a combination of biological factors, such as the length range of individuals sampled, their maturity stage, stomach fullness, diet, the presence of disease or parasite, and environmental conditions, such as temperature, pollution or fishing pressure (Franklin et al. 2009, Froese 2006, Ogunola et al. 2018).

In contrast to our results, previous studies described higher values of standard length, R^2 and b coefficients for *P. harpagos*, revealing that differences in local conditions, such as habitat, seasonal variation and stream area, can explain differences in length-weight relationships (Campos et al. 2020). Other factors, such as predation and intra and interspecific competition can affect reproduction, condition factor, and growth rate, thus influencing maximum length, intraspecific weight variation, and a and b coefficients, as observed here. For instance, *P. harpagos* fecundity and size is affected by predation (Gorini-Pacheco et al. 2018). Also, being a matrotrophic species (the mother provides nutrients to the developing embryos throughout pregnancy), pregnancy stage could affect the female weight (Zandonà et al. 2021) and thus be a source of variation in the LWR.

Moreover, our study observed a low R^2 for *P. maculicauda* in a stream impacted by pasture ($R^2 = 0.720$). In contrast, Campos et al (2020) found a $R^2 = 0.956$ for the same species in well preserved streams. This difference in R^2 values could indicate the influence of environmental conditions in LWR. Therefore, it is possible that the lower R^2 in impacted streams could be a consequence of differences in resource availability which is resulting in higher individual variability in fish weight. Other sources of intraspecific variation in fish weight that could be causing lower R^2 values are differences in reproductive status, condition factor, or seasonality (Campos et al. 2020, Lima et al. 2022). As for *S. marmoratus*, it is worth mentioning that its low sample size (Rio Guapiaçu: n = 5; Rio Ubatiba: n = 7) is because this is a rare species. Thus, this estimate must be treated with caution.

Anthropogenic threats to fish biodiversity from Atlantic Forest coastal streams are already known, caused especially by biological invasions and environmental alterations (Bezerra et al. 2019). Therefore, it is very important to gather information and increase our understanding of fish biology to trace effective conservation strategies and preserve the biodiversity of this biome.

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Author Contributions

Luisa R. Manna: Conceptualization; Methodology; Writing.

Eugenia Zandonà: Conceptualization; Statistical analysis; Writing.

Priscila Oliveira-Cunha: Conceptualization; Statistical analysis; Writing.

Rosana Mazzoni: Conceptualization; Methodology; Writing; Funding acquisition.

Conflict of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

All sampled fish were collected in accordance with the applicable Brazilian environmental legislation (collecting permit IBAMA/MMA 02022.002475/2006-10, authorization number 118/2006 – DIFAP/IBAMA). Voucher specimens, obtained in previous studies developed in the three studied streams, were placed in the collection of the Museu Nacional do Rio de Janeiro and Universidade Federal do Tocantins (MNRJ and UFT).

Data Availability

https://doi.org/10.48331/scielodata.ZLTY5L

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Short Communication

First record of melanism in the critically endangered Pampa cat (*Leopardus munoai*), an endemic species of the Pampa grasslands

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Abstract: We report the first record of a melanistic individual of the critically endangered Pampa cat (*Leopardus munoai*), from July 8th, 2021, at 10:45 am (coordinates 30.096288° S; 54.941139° W) in the area of the Brazilian army, known as Campo de Instrução Barão de São Borja (CIBSB), popularly known as Saicã.
Keywords: *Melanism, Uruguayan Pampas cat, Pampa.*

Primeiro registro de melanismo no criticamente ameaçado gato-pampeano (*Leopardus munoai*), uma espécie endêmica das áreas abertas do Pampa

Resumo: Este trabalho reporta o primeiro registro de melanismo do criticamente ameaçado de extinção gato-pampeano (*Leopardus munoai*), realizado em 8 de julho de 2021, às 10:45 da manhã. O registro foi obtido nas coordenadas 30.096288° S; 54.941139° W na área do exército brasileiro Campo de Instrução Barão de São Borja (CIBSB), popularmente conhecida como Saicã.
Palavras-chave: *Melanismo, gato-palheiro-pampeano, Pampa.*

Introduction

Polymorphic phenotypes are common in wild cats, with records of albinism, leucism and melanism in several species of felids from Africa, South America and Asia (Eizirik et al. 2003, Warrick 2010, McBride & Giordano 2010, Schneider et al. 2012, Silva 2017, Cho et al. 2013, Xu et al. 2013, Cronemberger et al. 2018). Melanism can be defined as the darkening of the background coloration of the integument (fur), which is genetically controlled. So far, all felid polymorphic mutations have been associated with either the ASIP (agouti signaling protein) or MC1R genes (Eizirik et al. 2003). There are some iconic cases of melanism such as in leopards (*Panthera pardus*) and jaguars (*Panthera onca*), which are called 'black panthers' (Eizirik et al. 2003, Schneider et al. 2012, Silva 2017, Silva et al. 2017). In Neotropical America, melanism is also frequently observed in small cats (Oliveira 1994, Eizirik et al. 2003, Oliveira & Cassaro 2005, Silva et al. 2016, Aximoff et al. 2021). In some cases, as in the jaguar, it is dominant, whereas in leopards it is recessive (Eizirik et al. 2003, Caro 2005). In this short communication, we report the first record of melanism in the Pampa cat (*Leopardus munoai*), an endemic species of the Pampa biome, and a small felid from the "*Leopardus colocola* complex", that has recently been recognized as a full species by Nascimento et al. (2020).

The Pampa cat or grassland Pampas cat, also known as Uruguayan or Muñoa's Pampas cat, is a small felid that measures between 70 and 96 centimeters in length, and weighs an average of 3.5 kg; however, its basic ecological needs are virtually unknown. Its distribution to the north of its range would be restricted by the forest massif of the Atlantic Forest, to the south and southwest by the Prata and Paraná Rivers, respectively, and to the east by the Atlantic Ocean (Nascimento et al. 2020). Thus, the species' range is restricted to the extreme south of Brazil (Pampa biome), Uruguay and a small strip of the Corrientes fields in the extreme northeast of Argentina. The part of the Pampa biome that spreads into the Brazilian territory measures approximately 178,000 km², which corresponds to 2.07% of the country as a whole, and is restricted to the state of Rio Grande do Sul. By making up 63% of the territory of the state, it is the dominant landscape (IBGE 2004, Overbeck et al. 2007). As a species, *L. munoai* is of high conservation concern (see Tirelli et al. 2021) and is going to be classified as Critically Endangered CR by the Brazilian authorities; however, this status has not been made official yet, and it is currently still classified under *Leopardus colocola* (as *L.c. munoai*) as Vulnerable (Queirolo et al. 2013, ICMBio unp. data). In this paper our intent is to report a new color morph identified for the Pampa cat (*Leopardus munoai*).

Materials and Methods

Camera trapping is being conducted in a public area belonging to the Brazilian army, known as Campo de Instrução Barão de São Borja (CIBSB), or popularly known as Saicã (Fig. 1), which covers 51,000 hectares, and is located between the municipalities of Rosario do Sul and Cacequi, in the state of Rio Grande do Sul, southernmost Brazil. The area comprises mostly native fields, with forest formations along water courses, adjacent to agriculture. In 2021, we deployed 6–9 camera traps spaced at ca. 500 m (400–600 m) from each other that focused on native fields that have been free from agriculture for at least 40 years. We followed well established camera-trapping protocols (as those described by de Oliveira et al. 2018, 2020).

Species identification was confirmed based on the concave head profile shown by both *L. munoai* and its sister species from the Cerrado, *Leopardus braccatus*. This is a diagnostic feature for identification of both species during camera-trapping (T.G. de Oliveira, pers. obs., F.D. Mazim pers. obs.). The ears are more pointed than the spotted species of *Leopardus*, which would also set it apart from a melanistic Geoffroy's cat, aside the bulkier body of the latter (T.G. de Oliveira, pers. obs., F.D. Mazim pers. obs.). Body shape and proportions are also used to distinguish them among the species (Oliveira & Cassaro 2005). Additionally, the researchers (TGO, FDM) have a vast experience with camera-trapping of small Neotropical felids (>5,000 records identified),

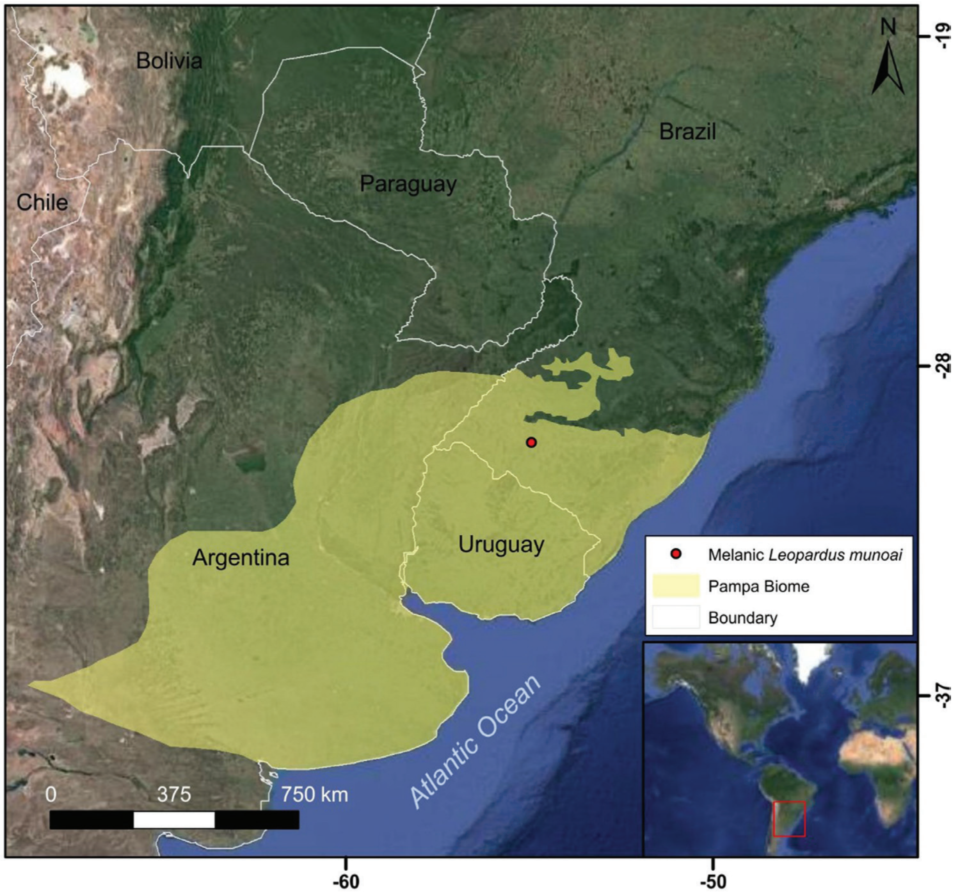

Figure 1. Location where the melanistic male specimen was recorded.

Figure 2. Melanistic male Pampa cat (*Leopardus munoai*) caught by camera-trap in the Pampa grasslands of Saicã (southernmost Brazil).

live-trapping (>200 individuals caught) as well as experience with several specimens of all Brazilian small cats in captivity.

Results and Discussion

After an effort of 1,080 trap-nights, a melanistic male Muñoa's Pampas cat was photo-trapped on July 8th, 2021, at 10:45 am (coordinates 30.096288° S; 54.941139° W) on the edge of a swamp, locally known as Laguna, which, in the 1970s, was intensively used to irrigate rice fields; a practice that no longer occurs within the limits of the CIBSB (Fig. 2). Another individual, with a plain, standard coat had been recorded earlier in the same area (May 27th 2021).

This is the first report of a melanistic *L. munoai* individual. However, melanism in the Pampas cat species complex (i.e., *Leopardus colocola* complex) has been recorded, mostly in the Pampas cats (*Leopardus braccatus*) found in the savannas of northern and central-western Brazil (Aximoff et al. 2021, T. de Oliveira pers. com.). In some sites, such as Mirador State Park in the savannas of Maranhão state, melanistic individuals can comprise up to > 90% of all records (T. de Oliveira pers. com.). However, we still cannot confirm whether melanism is a common event for *L. munoai*; but, based on records of road-killed individuals (N = 28, F. Mazim pers. obs.), it does not seem to be so. There is still a lot to be learned about this endemic felid of the Pampas.

Acknowledgments

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Author Contributions

Fábio Dias Mazim: data collection; analysis and interpretation; manuscript preparation and revision.

Paulo Guilherme Carniel Wagner: data collection; manuscript preparation and revision.

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João Fabio Soares: data collection; manuscript preparation and revision.

Tadeu Gomes de Oliveira: analysis and interpretation; manuscript preparation and revision.

Conflicts of Interest

The authors declare no conflict of interest.

Data Availability

All data are available in the paper.

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Article

A case of mass occurrence of *Sandalodesmus araujoi* (Schubart, 1946) in a municipality of São Paulo, Brazil and description of the heretofore unknown female (Polydesmida, Chelodesmidae)

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BOUZAN, R.S., MEANS, J.C., IVANOV, K., PUPIN, G.B., BRESCOVIT, A.D., INIESTA, L.F.M. **A case of mass occurrence of *Sandalodesmus araujoi* (Schubart, 1946) in a municipality of São Paulo, Brazil and description of the heretofore unknown female (Polydesmida, Chelodesmidae).** Biota Neotropica 23(3): e20231521. https://doi.org/10.1590/1676-0611-BN-2023-1521

Abstract: Somatic characters are shared by many Chelodesmidae groups, and generic placement and species identifications traditionally have been based on gonopodal morphology. Female genitalic characters have been largely neglected and are rarely photographed or illustrated. This is rather unfortunate as the morphology of female genitalia presents important characters and may be decisive for developing a more robust family classification. We describe the heretofore unknown female of *Sandalodesmus araujoi* (Schubart, 1946), previously known only from the male holotype collected in São Paulo, Brazil in December 1943; discuss the utility of female genitalic characters for species delineation in *Sandalodesmus*; and report the first case of a mass occurrence in the Chelodesmidae. While an attempt at a formal diagnosis of *Sandalodesmus* females based on genitalic characters is premature, the vulvar morphology of the three taxa examined in this study suggests that female genitalia are species-specific. Some characters (i.e., asymmetric valves, presence of digitiform projections and reduction of setae on the internal basal portion of the valves) are constant between the species, suggesting utility for generic-level delineation. Mass occurrences of millipedes are typically unpredictable and likely related to variations in environmental conditions and/or anthropogenic modifications of natural habitats. Although the mass occurrence of *S. araujoi* reported herein was only observed once, the event coincides with the mating period of millipedes during the rainy season in Brazil. On the other hand, the region where the species was found has been the target of intense urban development, including replacement of natural habitats with residential areas, which may have influenced its population dynamics.
Keywords: *millipedes; Neotropics; population outbreak; Sandalodesmini; swarming; taxonomy.*

Um caso de ocorrência em massa de *Sandalodesmus araujoi* (Schubart, 1946) em um município de São Paulo, Brasil e descrição da fêmea até então desconhecida (Polydesmida, Chelodesmidae)

Resumo: Os caracteres somáticos são compartilhados por muitos grupos de Chelodesmidae, e o posicionamento genérico e as identificações de espécies tradicionalmente têm sido baseadas na morfologia do gonópodo. Carateres genitais das fêmeas foram amplamente negligenciados e raramente são fotografados ou ilustrados. Isso é lamentável, pois a morfologia da genitália feminina apresenta características importantes e pode ser decisiva para o desenvolvimento de uma classificação mais robusta. Neste trabalho, descrevemos a até então desconhecida fêmea de *Sandalodesmus araujoi* (Schubart, 1946), anteriormente conhecida apenas pelo holótipo macho coletado em São Paulo, Brasil, em dezembro de 1943; discutimos a utilidade de caracteres genitais femininos para delineamento de espécies em *Sandalodesmus*; e relatamos o primeiro caso de ocorrência em massa para Chelodesmidae. Embora uma tentativa de diagnose formal para fêmeas de *Sandalodesmus* com base em caracteres genitais seja prematura, a morfologia vulvar dos três táxons examinados neste estudo, sugere que a genitália feminina é espécie-específica. Alguns caracteres (e.g. válvulas assimétricas, presença de projeções digitiformes e redução de cerdas na margem interna das válvas) são constantes entre as espécies do gênero, sugerindo utilidade para delineamento em nível genérico. Ocorrências em massa de milípedes são tipicamente imprevisíveis e provavelmente relacionadas a variações nas condições ambientais e/ou modificações antropogênicas de habitats naturais. Embora a ocorrência em massa de *S. araujoi* aqui relatada tenha sido observada apenas uma vez, o evento coincide com o período de reprodução dos milípedes durante a estação chuvosa no Brasil. Por outro lado, a região onde a espécie foi encontrada tem sido alvo de intenso desenvolvimento urbano, incluindo substituição de habitats naturais por áreas residenciais, o que pode ter influenciado sua dinâmica populacional.

Palavras-chave: *Milípede; piolho-de-cobra; Neotrópicos; surto populacional; Sandalodesmini; taxonomia.*

Introduction

With over 5,000 described species, Polydesmida is the most diverse order within the class Diplopoda and includes the two most species-rich families of millipedes, Paradoxosomatidae Daday, 1889 (approx. 1,000 described species) and Chelodesmidae Cook, 1895 (750+ described species) (Hoffman 1980, Shelley 2002, Brewer et al. 2012, Nguyen and Sierwald 2013, Enghoff et al. 2015). Chelodesmidae is divided into two subfamilies, Chelodesminae (139 genera) distributed across the Neotropical region, and Prepodesminae (37 genera) known from the Afrotropical and Palearctic regions (Hoffman 1980). Currently, 21 tribes are recognized within the Chelodesmidae, with 19 of them belonging to Chelodesminae, however, more than half of the described genera and species have yet to be assigned to a tribe (Bouzan et al. 2021).

Based chiefly on gonopodal characters, Hoffman (1982) proposed the tribe Sandalodesmini to include the South American *Oncoleptodesmus* Schubart, 1958 and *Sandalodesmus* Silvestri, 1902. Members of the tribe are small to moderately sized chelodesmids (25-45mm in length) with relatively slender bodies and reduced gonopods, characterized by the presence of a shield-like acropodite which conceals the solenomere in the lateral view, a subspatulate prefemoral process that partially envelops the acropodite, the presence of a spiniform process on the gonocoxa, and a modified, hook-like cannula (Hoffman 1982). *Sandalodesmus* differs from *Oncoleptodesmus* by the presence of only two macrosetae on the dorsal side of the gonocoxae and by the absence of spinulations on the lateral margin of the acropodite [except in *Sandalodesmus repandus* (Schubart, 1985); Silvestri 1902, Schubart 1958, Hoffman 1982, Rojas-Buffet et al. 2022]. *Sandalodesmus* includes 14 species distributed across Argentina, Brazil, Paraguay, and Uruguay and *Oncoleptodesmus* includes four species only known from the Brazilian state of Rio Grande do Sul (Attems 1931, 1938; Schubart 1958; Hoffman 1982; Rojas-Buffet et al. 2022). *Sandalodesmus* was reviewed by Hoffman (1982) and recently Rojas-Buffet et al. (2022) provided an updated key to the males.

Somatic characters are shared by many genera within the Chelodesmidae and generic placement and species identification have been traditionally based on gonopodal morphology (Hoffman 1971, Pena-Barbosa et al. 2013, Bouzan et al. 2017a). Female genitalic characters have been largely neglected, seldom examined, and rarely photographed or illustrated (Brölemann 1902; Schubart 1946; Hoffman 1990a, 1990b, 2000; Pena-Barbosa et al. 2013; Bouzan et al. 2017b, 2018a, 2018b). *Sandalodesmus* is no exception, and the females of only six of the 14 known species have been described in some, often very abbreviated, manner. To date, only the females of *Sandalodesmus joachimadisi* Rojas-Buffet and Bouzan, 2022 have been described in detail, including description of genitalic characters, and illustrated (Rojas-Buffet et al. 2022). This is rather unfortunate as the morphology of the female genitalia presents important characters and may be decisive for developing a more robust classification of the Chelodesmidae (see Hoffman 2012).

Mass occurrences (seemingly sudden increases in local abundance) in the Diplopoda are a result of natural cycles (reproduction swarming or lifecycle periodicity) or unpredictable changes in climate, resource availability, or fragmentation of natural habitat (David 2015, Niijima et al. 2021). Such events have been reported from Africa, Eurasia, and The Americas, and vary in magnitude from localized occurrences of hundreds of individuals to millions of individuals covering extensive areas (Cloudsley-Thompson 1949, Niijima et al. 2021). While small scale swarms can occasionally be a nuisance near human habitations in urban and suburban areas, large outbreaks have been reported to impact livestock, crop production, and even interfere with transportation (Cloudsley-Thompson 1949, Niijima et al. 2021). In an attempt to provide a more robust classification of millipede mass occurrences, Niijima et al. (2021) proposed the separation of these events into swarming (hundreds of individuals), mass emergence (thousands), and outbreak (millions), based on the number of individuals observed.

One of the largest millipede outbreaks ever recorded, occurred in West Virginia, USA in June, 1918 when an estimated 65,340,000 *Apheloria virginiensis corrugata* (Wood, 1864) covered 75 acres of farmland for over a month (Cloudsley-Thompson 1949). During this event, farmers were reportedly nauseated by the defensive chemicals released by the millipedes and cattle refused to graze in the impacted areas (Cloudsley-Thompson 1949). An equally impressive series of mass outbreaks have been reported for *Parafontaria laminata* (Attems, 1909) in Japan where mass occurrences of this species have caused multiple road and railroad obstructions between 1920 and 1984 (Niijima and Shinohara 1988, Niijima 1998, Niijima et al. 2021). Interestingly, *Parafontaria laminata armigera* Verhoeff, 1936 was recently shown to have a lifecycle akin to periodical cicadas with an outbreak event occurring every eight years (Niijima et al. 2021).

In Brazil, millipede population outbreaks are most commonly associated with non-native species including the Asian *Oxidus gracilis* (C. L. Koch, 1847) and *Orthomorpha coarctata* (Saussure, 1860)

(Polydesmida, Paradoxosomatidae), and more recently the Portuguese millipede, *Ommatoiulus moreleti* (Lucas, 1860) (Julida, Julidae) (Iniesta et al. 2020, 2021, 2022). Although all three species reach high densities in urban areas of southeastern Brazil, *O. gracilis* and *O. coarctata* have also become established in rural and natural environments, including forests, caves, and islands (Iniesta et al. 2021). There is little published information regarding population outbreaks of native millipedes in Brazil, except for those regarded as agricultural pests. The majority of these accounts concern species of Spirostreptida (Spirostreptidae and Pseudonannolenidae) in cultivated areas where they have been reported to cause damage to seedlings, tubers, and fruits (Schubart 1942; Boock and Lordello 1952; Lordello 1954; Boccardo et al. 1997, 2002). To date, there have been no published accounts of swarming or population outbreaks in the Chelodesmidae.

We report the first case of a mass occurrence in the Chelodesmidae and describe the heretofore unknown female of *Sandalodesmus araujoi* (Schubart, 1946), previously known only from the male holotype collected in the state of São Paulo, Brazil in 1943. In addition, we discuss the utility of female genitalic characters for species delineation in *Sandalodesmus* and provide additional information on male characters, including measurements and SEM images.

Materials and Methods

The material examined is deposited in the following collections (curators in parentheses): Instituto Butantan, São Paulo, Brazil (IBSP; A.D. Brescovit), Arachnida and Myriapoda collection of Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (FCE-Myr; M. Simó). Scanning electron micrographs were taken using a FEI Quanta 250 SEM (FEI, Oregon, USA) with an attached SLR digital camera at Instituto Butantan. Specimens selected for scanning electron imaging were cleaned two times (30 sec. each) ultrasonically, transferred to an ascending series of ethanol dilutions (70, 80, 90, and 100%), bathed for 15 minutes at each step, and critical-point dried. The samples were mounted on aluminum stubs and coated with gold in a sputter coater for 240 seconds. In addition, relevant morphological features were photographed with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereomicroscope and measured to the nearest 0.01 mm with Leica Application Suite ver. 2.5.0 (Leica Camera, Wetzler, Germany). Body-rings were measured in dorsal view, and antennomere lengths were measured in lateral view.

Female genitalic characters of *S. araujoi* (five specimens), *S. joachimadisi* Rojas-Buffet and Bouzan, 2022 (two specimens) and *Sandalodesmus* sp. (two specimens from Estação Ecológica Jureia/Itatins, São Paulo, Brazil) were examined and photographed in order to explore their utility in species delineation and classification.

Distribution maps were generated using the freeware DIVA-GIS ver. 7.5.0 (Hijmans *et al.* 2001).

Terminology of sexual and somatic characters follows Attems (1898), Brölemann (1900), Pena-Barbosa et al. (2013), and Koch (2015).

Results

The mass occurrence reported herein was brought to the lead author's attention in October 2021 when videos of the event were sent to him by Nicoly Calcagniti (Supplementary Material 1). Subsequently, several male and female specimens were received by the authors and identified as *S. araujoi*. The mass occurrence took place in the municipality of Pardinho (–23.0825, –48.3852), approx. 30 km southeast of the type locality of *S. araujoi* in the municipality of São Manuel (–22.7423, –48.6191) (Figure 1). According to the residents of the municipality, thousands of individuals were observed around house entrances, gardens, and on pavement in the morning and afternoon hours.

The locality where the mass occurrence took place is part of a transitional zone between the Cerrado and Atlantic Forest biomes in the state of São Paulo (Coutinho 2006). The area has a subhumid temperate climate and is characterized by a patchwork of herbaceous and forested habitats which have resulted from retractions and transgressions during the Quaternary (Coutinho 2006, Alvares et al. 2014, Smith and Mayle 2017). Since the second half of the 20th Century, the region has been severely impacted by human activities, including deforestation, farming practices, livestock production, and accelerated urbanization (Ratter et al. 1997).

Order Polydesmida Pocock, 1887

Family Chelodesmidae Cook, 1895

Subfamily Chelodesminae Cook, 1895

Tribe Sandalodesmini Hoffman, 1982

Genus *Sandalodesmus* Silvestri, 1902

Sandalodesmus araujoi (Schubart, 1946)

(Figures 1–17)

Leptodesmus araujoi Schubart 1946: 171, figure 4 (male holotype from São Manuel [-22.7423, -48.6191], São Paulo, Brazil, 09–11. xii.1943, R. L. Araujo leg., deposited at MZSP, examined); Schubart 1955: 516.

Leptodesmus (Gonioleptodesmus) araujoi:-- Schubart 1958: 29.

Gonioleptodesmus araujoi:-- Hoffman 1967: 34.

Sandalodesmus araujoi:-- Hoffman 1982: 251; Bouzan et al. 2018c: 11; Rojas-Buffet et al. 2022: 266.

New record. BRAZIL, São Paulo, Pardinho; –23.0825, –48.3852; 900 m; October 2021; N. Calcagniti leg.; in urban areas, around house entrances, gardens, and on pavement; 1♂ (IBSP 14277); 1♀ (IBSP 14278); 6♂♂, 6♀♀ (IBSP 14279).

Diagnosis. Males of *S. araujoi* can be separated from those of *Sandalodesmus gasparae* (Schubart, 1944) (Schubart 1944, figures 22-23) and *Sandalodesmus hippocampus* (Schubart, 1944) (Schubart 1944, figures 25-26), the only other *Sandalodesmus* species known from the state of São Paulo, by the presence of a prominent subtriangular, secondary process on the lateral side of the acropodite (Figures 4A, C). In addition, males of *S. araujoi* can be separated from those of *Sandalodesmus salvadorii* (Silvestri, 1895), the only other member of the *salvadorii* species group (see Hoffman [1982]), based on the rounded, mesally curving acropodite (Figures 4A, C), which is subtriangular and curving cephalad in *S. salvadorii* (Hoffman 1982, Rojas-Buffet et al. 2022).

Description. Male (new data; IBSP 14277): With characteristics typical for the genus. Coloration in life: body rings dark brown,

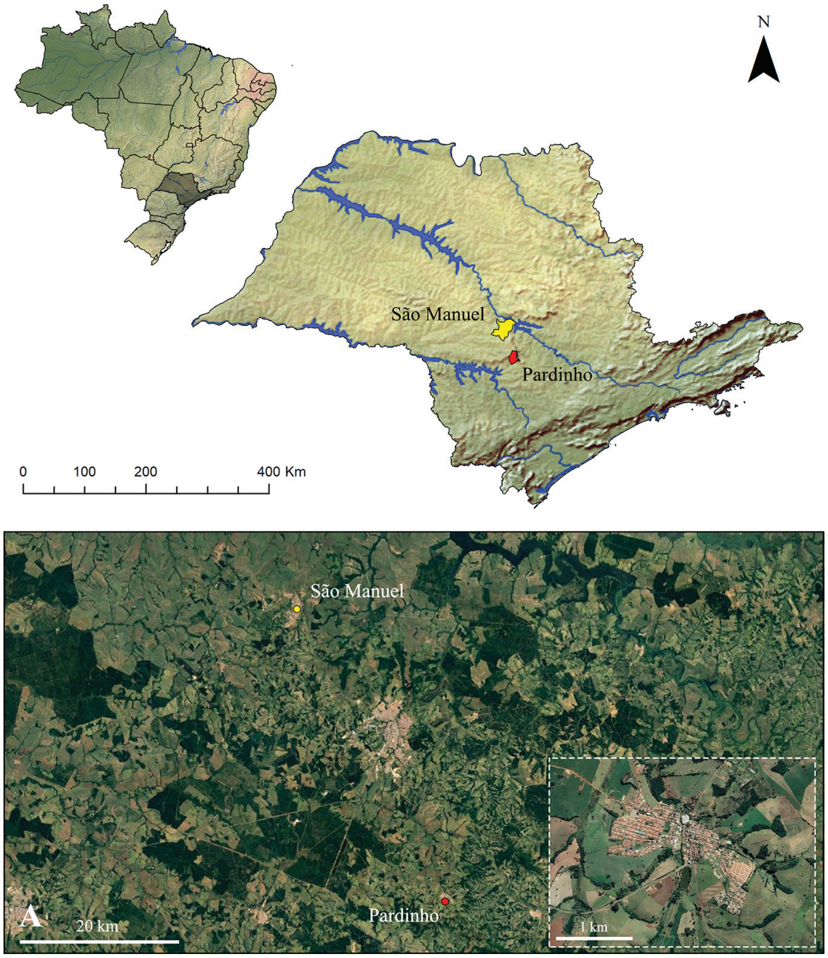

Figure 1. Known distribution of *S. araujoi* with the São Manuel type locality shown in yellow and the new record from Pardinho shown in red.

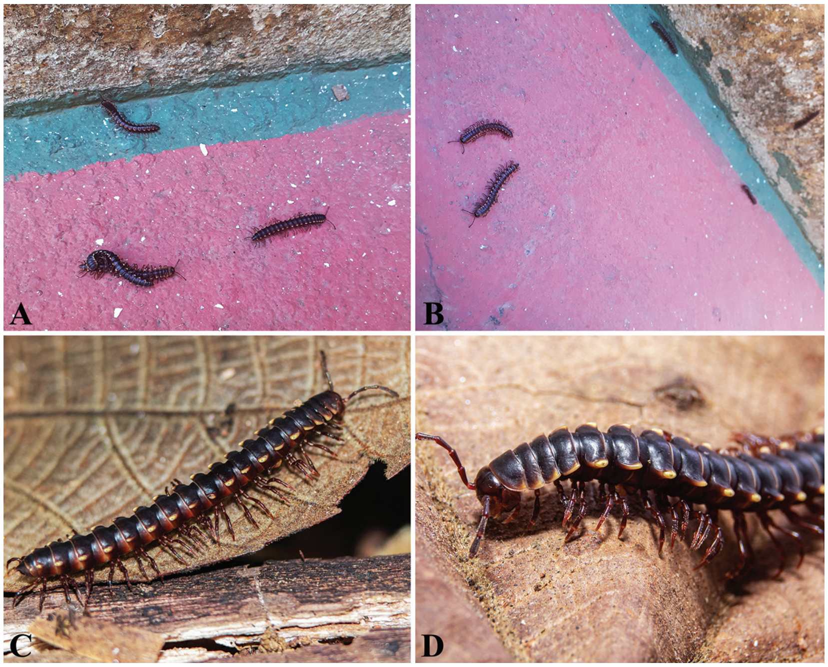

Figure 2. A–D. Living specimens of *S. araujoi* from Pardinho, São Paulo, Brazil.

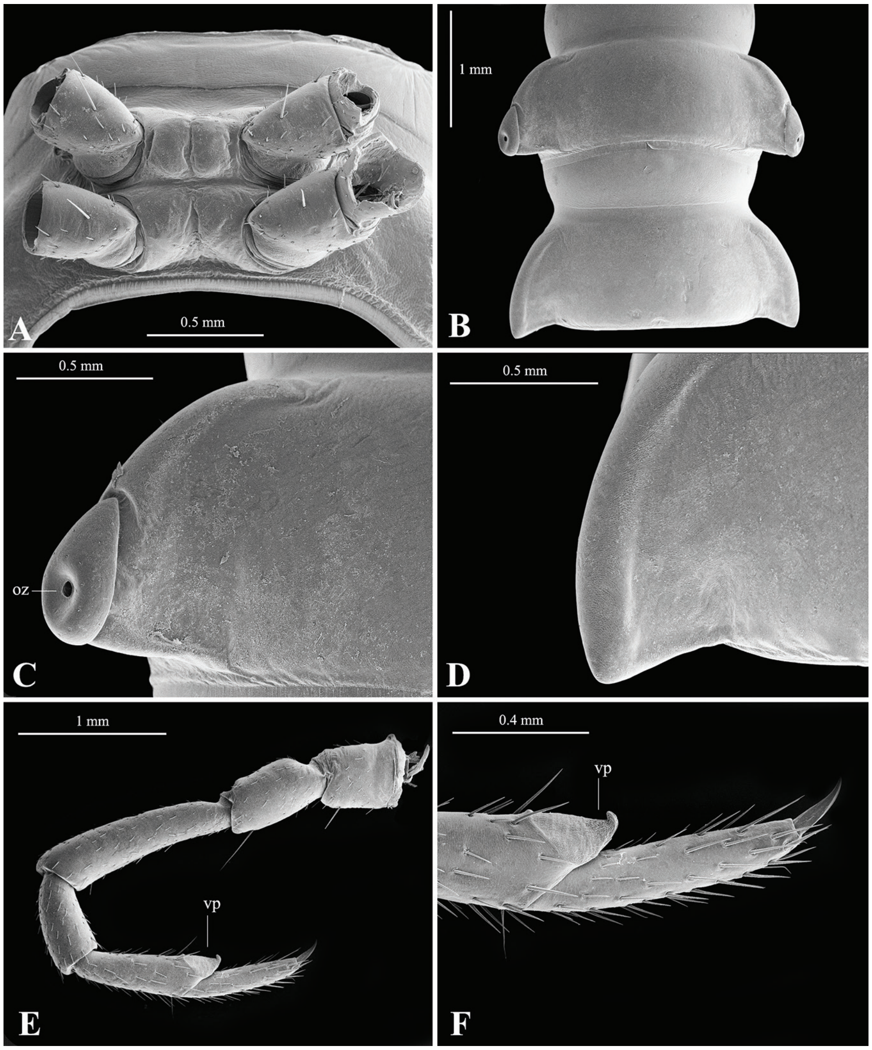

Figure 3. A–F. SEM images of somatic characters of *S. araujoi* (IBSP 14279). A, Projections of sternite 4, ventral view. B, Midbody rings, dorsal view. C, Paranota with ozopore, dorsal view. D, Paranota, dorsal view. E, Midbody leg. F, Detail of tibial ventral pad. Abbreviations: vp= ventral pad, oz= ozopore.

head, antennae, and legs reddish-brown, paranota tips yellowish (Figures 2A–D). *Head:* epicranial macrosetae 2–2, interantennal macrosetae 1–1, frontal macrosetae 1–1. *Body:* rings smooth; paranota subtriangular, with standard polydesmidan pore formula (5, 7, 9, 10, 12, 13, 15–19; Figures 3B–D); ozopores situated posteriorly (Figure 3C); sternite of 4th body ring with two pairs of partly appressed projections (Figure 3A). *Legs:* with ventral tibial pads, except for the last leg pair (Figures 3E–F).

Gonopods: prefemoral process (pfp) subtriangular, slightly twisted, and parallel to acropodite (ap) (Figures 4A, C); cannula (ca) hook-shaped (Figure 4C); seminal groove (sg) S-shaped along the acropodite, ending at apex of solenomere (Figure 4C); prefemoral region (pf) densely setose (Figures 4A, C); acropodite (ap) broad, elongated, strongly curved mesad (Figures 4A, C), with part of its margin serrated mesally (Figures 4A–B, white arrow), and with a prominent subtriangular secondary process; solenomere (s) sickle-shaped, curved mesad (Figure 4C).

Measurements (mm): Body: total length (n = 3), average = 34.1 (range = 29.1 – 38.5); width of 10th body ring (n = 3), average = 3.6 (range = 3.3–3.8). Antennomere lengths (1–7): 0.33, 0.91, 0.87, 0.80, 0.88, 0.82, 0.21. Telson length: 0.6.

Female (IBSP 14278): Coloration in life as in male. Similar to male in general body outline and somatic characters, except sternite of 4th body ring with less conspicuous and separate projections, all remaining sternites and all legs without modification. Posterior margin of vulvar aperture smooth, without projections. *Vulvae* (Figures 4D–F): densely setose, ovoid in ventral view and subrectangular in lateral view. External and internal valves asymmetrical, projecting ventrad. External valve (Ev) projecting distad, distinctly longer than the internal valve (Iv). Internal margins of valves irregular medially, with digitiform projections (Figure 4F). Internal basal portion of valves, in ventral view without setae. Operculum (Op): small, flattened, with setae at the base, approximately 1/6 size of valves.

Measurements (mm): Body: total length (n = 3), average = 30.1 (range = 29.2 – 30.8); width of 10th body ring (n = 3), average = 3.3 (range = 3.2–3.4). Antennomere lengths (1–7): 0.32, 0.81, 0.67, 0.70, 0.74, 0.73, 0.20. Width of posterior margin of vulvar aperture 1.4. Vulvae: ventral length 0.88, ventral width 0.53. Valves asymmetrical.

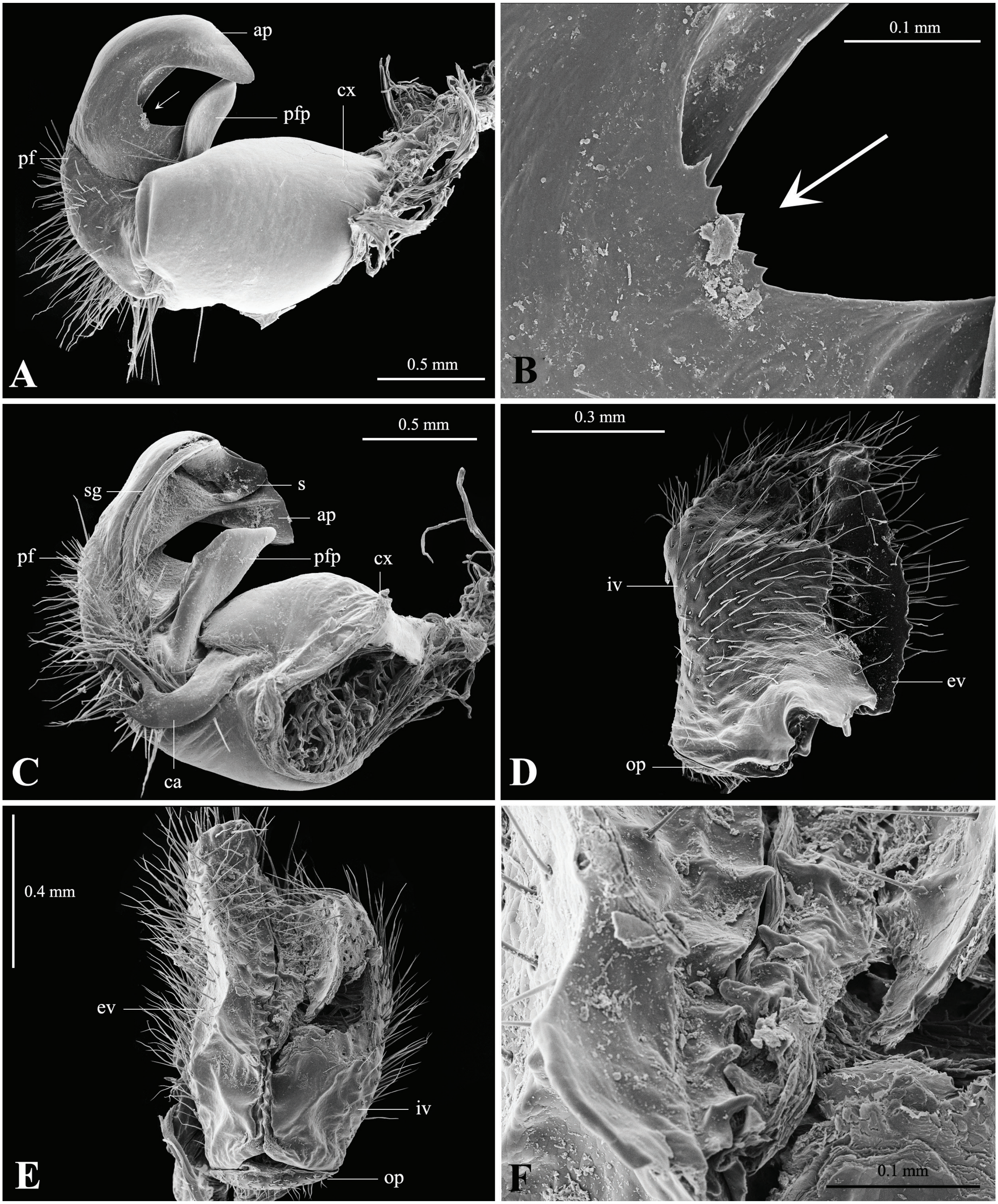

Figure 4. A–F. SEM images of genitalic characters of *S. araujoi* (IBSP 14279). A, Left gonopod, ectal view. B, Detail of mesal portion of the acropodial process, ectal view. C, Right gonopod, mesal view. D, Left vulva, ectal view. E, Right vulva, ventral view. F, Detail of the junction of the valves, ventral view. Abbreviations: ap= acropodital process, ca= cannula, cx= gonocoxa, ev= external valve, iv= internal valve, op= operculum, pf= prefemur, pfp= prefemoral process, s= solenomere, sg= seminal groove. The subtriangular secondary process is hidden by the prefemoral process in ectal and mesal view.

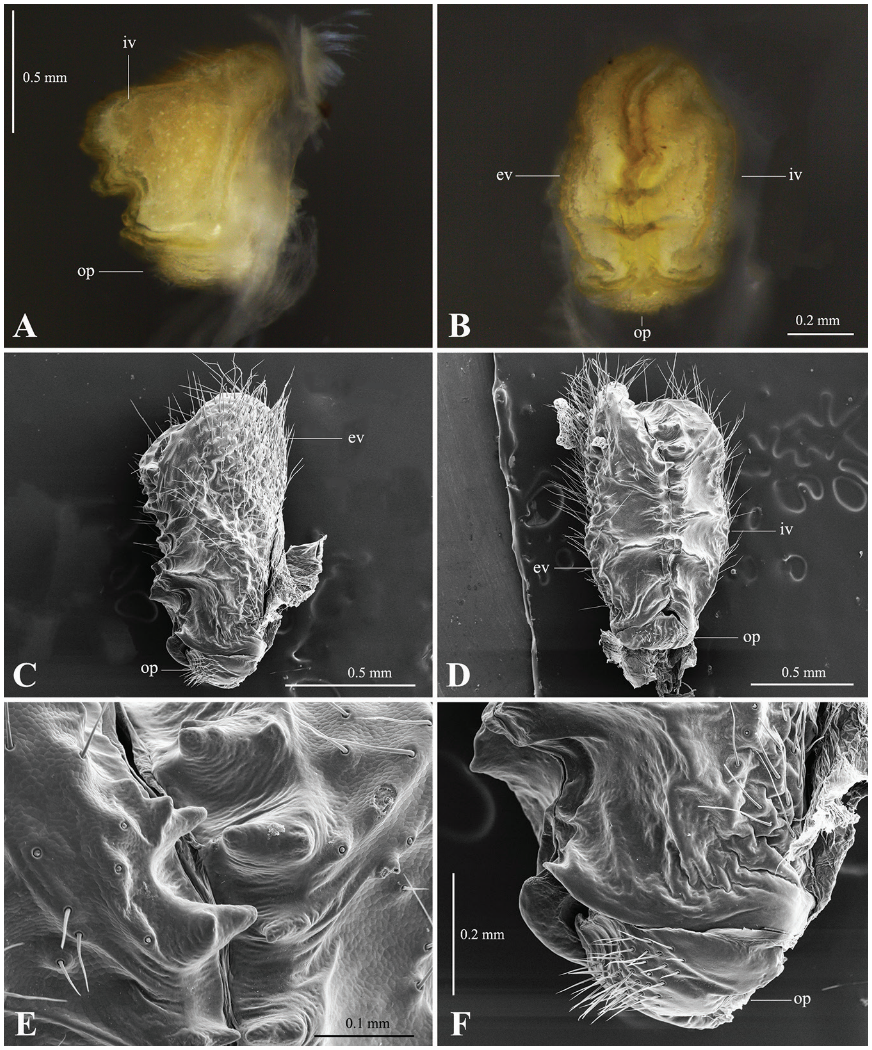

Figure 5. A–F. Steromicroscope (5A–B) and SEM images (5C–F) of vulvae of *Sandalodesmus* species: A, Right vulva of *S. joachimadisi* (FCE-Myr 0664), ectal view; B, Right vulva of *S. joachimadisi* (FCE-Myr 0664), ventral view. C, Left vulva of *Sandalodesmus* sp. (IBSP 3741), ectal view. D, Right vulva of *Sandalodesmus* sp. (IBSP 3741), ventral view. E, Detail of the junction of the valvae of *Sandalodesmus* sp. (IBSP 3741), ventral view. F, Detail of the operculum of *Sandalodesmus* sp. (IBSP 3741), ectal view. Abbreviations: ev= external valve, iv= internal valve, op= operculum.

External valve: lateral length 0.72, lateral width 0.61. Internal valve: lateral length 0.61, lateral width 0.59. Operculum: ventral length 0.14, ventral width 0.34. Telson length: 0.6.

In comparison to *S. araujoi*, the size difference between the external and internal valves of *Sandalodesmus* sp. (from Estação Ecológica Jureia/Itatins, São Paulo, Brazil) is less pronounced, and those of *Sandalodesmus* sp. have larger and fewer digitiform projections which continue to the apical portion of the valves (Figures 4E-F; 5B, 5D-F). In addition, the vulvae of *Sandalodesmus* sp. have a pronounced horizontal ridge spanning both valves and delineating the bottom third of each (Figures 5C–D). As compared to the previous two species, the valves of *S. joachimadisi* are relatively symmetrical, with only a slight enlargement of the external valve, and with fewer and more robust digitiform projections on the internal margin (Figures 5A–B). In addition, the lateral profile of the valves of *S. joachimadisi* is distinctly subtriangular while those of both *S. araujoi* and *Sandalodesmus* sp. are subrectangular, narrower near the operculum and widening towards the apex (Figures 4D, 5A, 5C).

Discussion

Although numerous collection events have targeted the area surrounding the type locality of *S. araujoi*, until the mass occurrence reported herein, this species was known only from the single male holotype collected in the municipality of São Manuel in December 1943 (Schubart 1946).

Millipede female genitalia undoubtedly contain valuable taxonomic information, however, they have been historically neglected and have been rarely included in species descriptions. Genitalic characters of female *Sandalodesmus* remain poorly known, and only those of *S. joachimadisi* have been described and properly illustrated (Rojas-Buffet et al. 2022: figure 3D). While an attempt at a formal diagnosis of females based on genitalic characters is premature, the vulvar morphology of the three taxa examined herein suggests that *Sandalodesmus* female genitalia are species-specific. In addition, some characters, such as the asymmetric (to different degrees) valves, and the presence of digitiform projections and the reduction or absence of setae on the internal basal portion of the valves, are constant between the species, suggesting utility for generic-level delineation. Additional studies on the morphology of *Sandalodesmus* female genitalia are needed to assess their systematic importance.

With the exception of the population outbreaks of the Japanese *P. laminata armigera*, mass occurrences of millipedes are typically unpredictable and likely related to variations in environmental conditions and/or anthropogenic modifications of natural habitats. Although the mass occurrence of *S. araujoi* reported herein was only observed once, the timing of the event coincides with the mating period of millipedes during the rainy season (October–April) in Brazil (see Alvares et al. 2013). On the other hand, the region where the species was found has been the target of intense urban development, including replacement of natural vegetation with residential areas, which may have influenced its population dynamics. More detailed studies are needed to tease apart the factors contributing to these largely unpredictable events.

The original communities of the Cerrado and the Atlantic Forest in southeastern Brazil, two of the world's premier biodiversity hotspots, have been severely altered by anthropogenic activities, such as medium to large-scale farming practices, livestock production, and accelerated urbanization, and are rapidly disappearing (Fonseca 1985, Durigan et al. 2007). To date, approximately 50% of the Cerrado has been destroyed by human activities (Rodriguez-Zorro et al. 2022), and only 10% of the original vegetation of the Atlantic Forest remains (Colombo and Joly 2010, Joly et al. 2014, Rezende et al. 2018). The region, long known for its vertebrate and invertebrate diversity and high levels of endemicity, was also recently shown to contain the highest species richness and the highest concentration of threatened Spirostreptida in Brazil making its conservation vital for the protection of numerous plant and animal taxa (Iniesta et al. 2023).

Supplementary Material

The following online material is available for this article:
Supplementary Material 1

Acknowledgments

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Kaloyan Ivanov: data collection; manuscript preparation and revision.

Giovanni B. Pupin: manuscript preparation and revision.

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Conflicts of Interest

The authors declare that there is no conflict of interest related to the publication of this manuscript.

Data Availability

The data used in this study are available at Biota Neotropica Dataverse

https://doi.org/10.48331/scielodata.W9CXON

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Article

One more place to call home: the invasive bivalve *Mytilopsis leucophaeata* reaches the Maricá-Guarapina lagoon system (Rio de Janeiro, Brazil)

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Abstract: *Mytilopsis leucophaeata* is an estuarine bivalve native from the Gulf of Mexico and Southeast USA, and it was introduced in Europe, Asia, Caribbean, South America and Northeast USA, showing massive colonization skills. In Brazil, the single invasion records of *M. leucophaeata* occur in the city of Rio de Janeiro, i.e., in the Rodrigo de Freitas Lagoon and in the Marapendi Lagoon. We conducted a new series of fieldworks in estuaries from the Rio de Janeiro state in order to evaluate the propagation of this invasive bivalve, aiming sites with proper salinities for the establishment of *M. leucophaeata*. A new record is given for the Maricá-Guarapina lagoon system, where *M. leucophaeata* mainly colonizes hard substrata (such as piers and rocks), reaching a mean density up to 43,375 specimens/m^2; however, aggregates of *M. leucophaeata* were also observed in the soft substratum. Based on mitochondrial sequences, the taxonomic identification of the invasive bivalve was confirmed. The associated fauna to the agglomerates of *M. leucophaeata* in the lagoon system comprises amphipods, barnacles, tanaidaceans, isopods, crabs, polychaetes and snails. The expansion of *M. leucophaeata* requires a continuous investigation due to the great circulation of boats in the littoral of the Rio de Janeiro state and the increased chance of new introductions.

Keywords: *Biological invasion; secondary dispersion; ecosystem engineer; associated fauna; estuary; Dreissenidae.*

Mais um lugar para chamar de casa: o bivalve invasor *Mytilopsis leucophaeata* alcança o sistema lagunar Maricá-Guarapina (Rio de Janeiro, Brasil)

Resumo: *Mytilopsis leucophaeata* é um bivalve estuarino originário do Golfo do México e Sudeste dos EUA, tendo sido introduzido na Europa, Ásia, Caribe, América do Sul e Nordeste dos EUA, e apresentando massiva capacidade de colonização. No Brasil, os únicos registros de invasão de *M. leucophaeata* ocorrem no município do Rio de Janeiro, i.e., na Lagoa Rodrigo de Freitas e na Lagoa de Marapendi. Este estudo propõe um novo levantamento de campo em estuários fluminenses para avaliar a propagação desse bivalve invasor, visando locais com salinidade propícia para o estabelecimento de *M. leucophaeata*. Um novo registro é feito para o complexo lagunar Maricá-Guarapina, onde *M. leucophaeata* coloniza principalmente substratos duros (como píers e rochas), chegando a uma densidade média de 43.375 indíviduos/m^2; porém, agregados de *M. leucophaeata* também foram observados em substrato inconsolidado. Com base em sequências mitocondriais, a identificação taxonômica do bivalve invasor foi confirmada. A fauna associada aos aglomerados de *M. leucophaeata* no complexo lagunar compreende anfípodes, cracas, tanaidáceos, isópodes, caranguejos, poliquetas e gastrópodes. A expansão de *M. leucophaeata* demanda uma investigação contínua devido ao alto fluxo de embarcações no litoral fluminense e elevada probabilidade de novas introduções.

Palavras-chave: *Invasão biológica; dispersão secundária; espécie engenheira; fauna associada; estuário; Dreissenidae.*

Introduction

Mytilopsis leucophaeata (Conrad, 1831) is an estuarine bivalve with planktotrophic development and massive colonization in several types of hard substrata (Verween et al. 2010, Kennedy 2011), but occasionally also forming agglomerates in soft substrata (Fernandes et al. 2020, Rodrigues et al. 2022). The required salinity for the survivorship and reproduction of *M. leucophaeata* are below 18–21 ppt (Kennedy 2011, Van der Gaag et al. 2016, Maia-Neto et al. 2020). This species is native from the Gulf of Mexico and Southeast USA, where it has low densities, and it was introduced in Europe, Asia, Caribbean, South America and Northeast USA (Fernandes et al. 2018, 2021, Lodeiros et al. 2019, Zhulidov et al. 2021, Rodrigues et al. 2022). In Brazil, the confirmed records of *M. leucophaeata* are in the city of Rio de Janeiro, i.e., in the Rodrigo de Freitas Lagoon and in the Marapendi Lagoon (Rizzo et al. 2014, Fernandes et al. 2020). This bivalve may form huge aggregates in invaded sites; for example, at the Rodrigo de Freitas Lagoon, a mean density of up to 84,560 specimens/m^2 was recorded (Maia-Neto et al. 2020), enabling the filtration of a large amount of water (Neves et al. 2020). The arrival of *M. leucophaeata* in a new site may alter the nutrient cycling and the structure of the benthic, planktonic and nektonic communities, acting as an ecosystem engineer (Kennedy 2011, Neves et al. 2020, Rodrigues et al. 2021), and may promote economic losses (Rajagopal et al. 1997, Verween et al. 2010, Florin et al. 2013, Lodeiros et al. 2019).

The primary dispersal (long distance) of *M. leucophaeata* into new areas may occur through the transference of larval forms by the inadequate discharge of ballast water, whereas the incrustation of specimens in the hull of a ship or boat may also promote secondary dispersion (medium or short distance) (Kennedy 2011, Fernandes et al. 2018, 2020, 2021). Even with the existence of Brazilian laws that regulate the discharge of ballast water (Normam-20/DPC), the surveillance is inefficient. Because of that, Brazil is a great receptor of marine and estuarine non-native species, comprising diverse taxonomic groups and with the constant record of new species (Teixeira & Creed 2020), which brings a series of damages (sometimes irreversible) to the native biodiversity (Pysek et al. 2020).

This study aims to improve the knowledge about the distribution of *M. leucophaeata* in the Rio de Janeiro state, complementing the previous data of Fernandes et al. (2020). After a new series of fieldworks, guided to sites with proper salinities for the establishment of the bivalve, a new record is provided, leading us to study the composition of the fauna associated to agglomerates of *M. leucophaeata* and how some environmental and anthropic aspects may influence the distribution of this invader.

Material and Methods

1. *Study area*

The study area comprises part of the littoral of Rio de Janeiro state (Figure 1), additional to the data of Fernandes et al. (2020). Samplings were mainly performed at 'Região dos Lagos' (Figure 1A; including the Maricá-Guarapina lagoon system, the Saquarema lagoon system and the lagoons of Jaconé and Jacarepiá) and at Sepetiba Bay (Figure 1B; including the vicinities of the Port of Itaguaí, the mouth of Guandu River and a mangrove area at Guaratiba). In addition, the Jacuecanga River (city of Angra dos Reis) was also visited (Figure 1B).

Sepetiba Bay is a semi-closed waterbody with an area of 305 km^2, receiving the discharge of 12.6 to 14.5 million m^3 of freshwater per day, mainly through the canal of São Francisco and the rivers Guarda, Guandu and Mazomba-Cação (Carreira et al. 2009). This bay receives impacts through the polluted rivers, the local presence of industries and the dense urbanization, including domestic/industrial sewage and leakage of heavy metals (Ribeiro et al. 2015, PACS 2015, Rodrigues et al. 2017). The Port of Itaguaí was inaugurated in 1982 under the

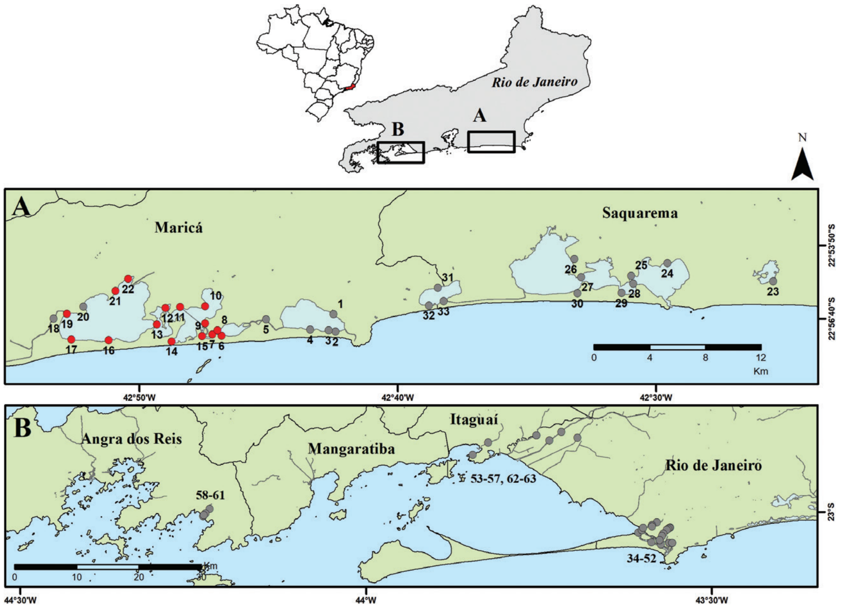

Figure 1. Map of Rio de Janeiro state with detailed location of the sampling stations: A- Municipalities of Maricá and Saquarema; B- Municipalities of Angra dos Reis, Mangaratiba, Itaguaí and Rio de Janeiro. Circles indicate absence (grey) or presence (red) of *Mytilopsis leucophaeata*, whether by live specimens or empty shells/valves. Coordinates available in Appendix 2.

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old name Port of Sepetiba, having an important role in the transport of iron ore; it was the sixth Brazilian port in terms of cargo transport in 2021 (ANTAQ 2022). However, the growing expansion of the port has substantially increased the socio-environmental impacts in the area (PACS 2015, Cordeiro & Amaral 2017).

The conservation unit 'Reserva Biológica Estadual de Guaratiba' (RBG) was created in 1974 and aims to preserve a mangrove area of 360,000 m² in the city of Rio de Janeiro, having a strong influence of the Sepetiba Bay (INEA 2021a). Such ecosystem has an evident environmental value (high biodiversity; sites of resting and feeding for migratory birds; prevention of flooding; source of organic matter for adjacent waters), in addition to economic (artisanal fishing; crab and mussel collectors) and historical (containing 18 'sambaquis', i.e., pre-Columbian shell mounds) values (INEA 2021a). Among the anthropic impacts in the area, there are illegal hunting and fishing, construction of irregular houses, domestic sewage without any prior treatment, and tourism.

At the Ilha Grande Bay, the Jacuecanga River discharges at ~5.5 km away from the fourth Brazilian port (Terminal Aquaviário de Angra dos Reis) in terms of cargo transport at 2021 (ANTAQ 2022). About 0.5 km away from the mouth of the Jacuecanga River, there are several shipyards and a large marina (Verolme), which may influence the arrival of exotic species.

The Maricá-Guarapina lagoon system covers a total area of ~35 km² and it is composed of four interconnected waterbodies: Maricá (~18 km²), Barra (~8 km²), Padre (~2 km²) and Guarapina (~6 km²) (Cruz et al. 1996). The system connects to the sea through the Ponta Negra canal, an artificial canal constructed in 1951 and which is often silted (Rodrigues et al. 2015), and with a minor drainage canal that ends at the Itaipuaçú Beach. Historically, the lagoon system had cycles of opening and closure of the sea connection through the site 'Barra da Emergência', usually regulated by anthropic means (Oliveira et al. 1955). The lagoon system shows a broad salinity variation according to weather conditions and the opening period of the Ponta Negra canal (Silvestre et al. 2017), with a mean of 18 ppt (Franco et al. 2019), although the inner waterbody (Maricá Lagoon) often shows salinity levels close to zero (Guerra et al. 2011, Laut et al. 2019). The lagoon system has great socioeconomic importance for the city of Maricá, due to several activities related to recreation, tourism and fishing. However, the growing urbanization at the margins of the lagoon system has increased sediment and sewage input, which, associated with the low depth levels and reduced water renovation, leads to its silting up and eutrophication (Cruz et al. 1996, Rodrigues et al. 2015, Silvestre et al. 2017, Laut et al. 2019, Toledo et al. 2021). Other near lagoons show different salinity levels, such as the euhaline Saquarema lagoon system (mean: 27–33 ppt) and the hyperhaline Araruama Lagoon (mean: 46–48 ppt) (Franco et al. 2019). Atypical years may greatly alter such conditions (Moreira-Turcq 2000) and differences in the salinity between dry and wet seasons might be high (Mendes & Soares-Gomes 2011, Dias et al. 2017).

2. *Sampling and laboratory procedures*

Fieldworks were conducted on seven events (without repetition of sites) between August/2021 and February/2022, in search of new areas for the establishment of *M. leucophaeata*. We mainly investigated hard substrata (natural, such as rocks and mangrove roots, or artificial, such as piers and decks) in estuaries and lagoons, with a careful visual inspection; empty valves were also searched in the sediment. Water temperature and salinity were measured through the equipment Hanna Instruments HI98319. When present, aggregates of *M. leucophaeata* were sampled (three replicates) by scraping the substratum with a spatula and a square sampler of 0.04 m², stored in plastic bags and kept in a freezer for posterior analyses. We used a 5 L Van Veen grab in the soft substratum in only one event (Guaratiba, 30/August/2021). At the same event, some agglomerates of the 'sururu' mussel *Mytella strigata* (Hanley, 1843) were collected in order to evaluate a possible presence of *M. leucophaeata* nested within it; the fauna associated to this mussel is shown in Appendix 1, regarding the few available data from this estuary.

At the laboratory, individuals of *M. leucophaeata* with soft parts were counted, and the shell length of each specimen was measured through a digital caliper rule (0.01 mm precision). The associated fauna was sorted, identified and stored in ethanol 70%, to be deposited in the scientific collections of Museu Nacional, Universidade Federal do Rio de Janeiro (MN/UFRJ) and Universidade do Estado do Rio de Janeiro (UERJ); the taxonomic identifications were confirmed by specialists (see 'Acknowledgments'). Photographs were conducted in a Leica DFC450 camera coupled to a stereoscopic Leica M205C. Mantle tissues were removed from eight specimens of *M. leucophaeata* and stored in 100% ethanol, for the genetic confirmation of the invasive lineage.

3. *Genetic procedures*

DNA was extracted with a Qiagen DNeasy Blood and Tissue kit, with the quality of the extraction measured through a Nanodrop 2000 spectrophotometer. We followed the procedures of Fernandes et al. (2021) for the partial amplification of the COI (cytochrome c oxidase subunit 1) gene, using primers HCO2198-LCO1490 (Folmer et al. 1994) and the thermocycling profile: initial denaturation at 95°C (5′); 37 cycles of denaturation at 95°C (45″), annealing at 48°C (45″), extension at 72°C (1′30″), followed by a final extension at 72°C (5′). Sequences were merged in *contigs* using the software MEGA 7, and aligned with MUSCLE. The eight new COI sequences were compared with 23 sequences of *M. leucophaeata* and three sequences of *Mytilopsis* cf. *sallei* (Récluz, 1849) retrieved from the GenBank, with a final alignment of 658 nt. Trees were generated by Bayesian Inference (MrBayes 3.2.7) and Maximum Likelihood (PhyML 3.0), following the procedures in Fernandes et al. (2021).

4. *Ecological analyses*

The species richness associated to the agglomerates of *M. leucophaeata*, as well as diversity (Shannon-Weaver, H') and equitability (Pielou, J') of the associated fauna were compared between the three sites where agglomerates were sampled. The density of *M. leucophaeata* specimens per class size was calculated for each of the three sites where agglomerates were sampled. The spatial abundance of *M. leucophaeata* was interpolated (Inverse Distance Weighted – IDW) regarding the distance to sampled sites, in a map elaborated in a GIS software.

Results

The single estuary in which *Mytilopsis leucophaeata* was found is the Maricá-Guarapina lagoon system, more specifically at the Maricá and Barra lagoons, with a few live individuals found near the connection between Barra and Padre lagoons (Figures 1–2; Appendix 2). At the Padre Lagoon, we found only empty valves of *M. leucophaeata*, whereas at the Guarapina Lagoon there were no traces of the invader. The maximum salinity measured at this lagoon system during the sampling event was 17.3 ppt, with a minimum of 2.2 ppt (Appendix 2). Live specimens of *M. leucophaeata* were observed in different habitats in the lagoon system, such as bridge pillars, wood and PVC (polyvinyl chloride) decks, rocks and even at the soft sediment (Figure 3). At stations 16–17, where live specimens of *M. leucophaeata* were observed in the soft sediment, they were originally adhered to small pieces of pebble and empty valves of *Anomalocardia flexuosa* (Linnaeus, 1767) (Figure 3F-G), with a subsequent colonization and formation of agglomerates above the small nucleus of *M. leucophaeata*. Owing to the scarcity of mangrove trees in this area, we could not search specimens of *M. leucophaeata* in this substratum.

The invasive bivalves at the Maricá-Guarapina lagoon system reached a maximum shell length of 28.1 mm, near the record of this

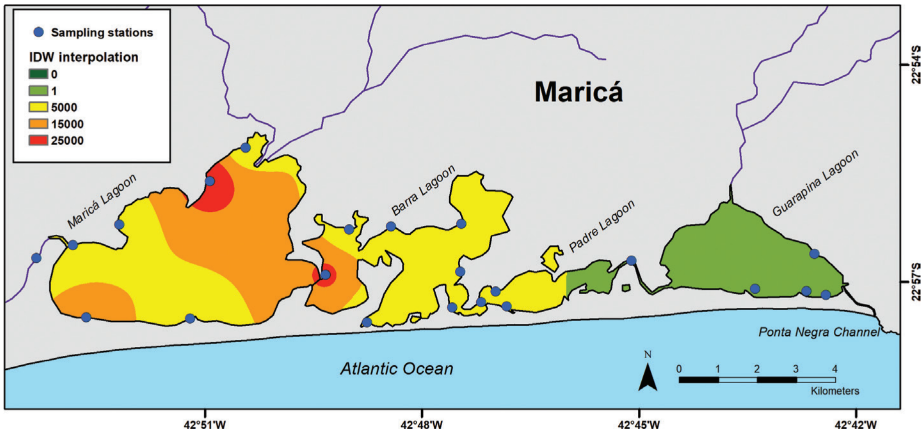

Figure 2. Interpolated density of *Mytilopsis leucophaeata* in the Maricá-Guarapina lagoon system.

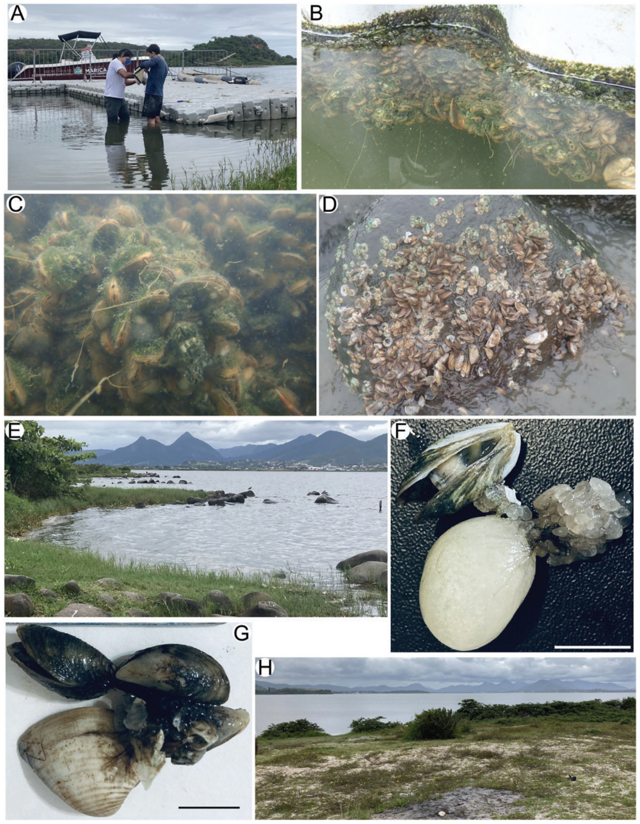

Figure 3. Sites of occurrence of *Mytilopsis leucophaeata* at the Maricá-Guarapina lagoon system; PVC deck – sta. 14 (A-C), rocks – sta. 21 (D-E), soft sediment – sta. 17 (F-H).

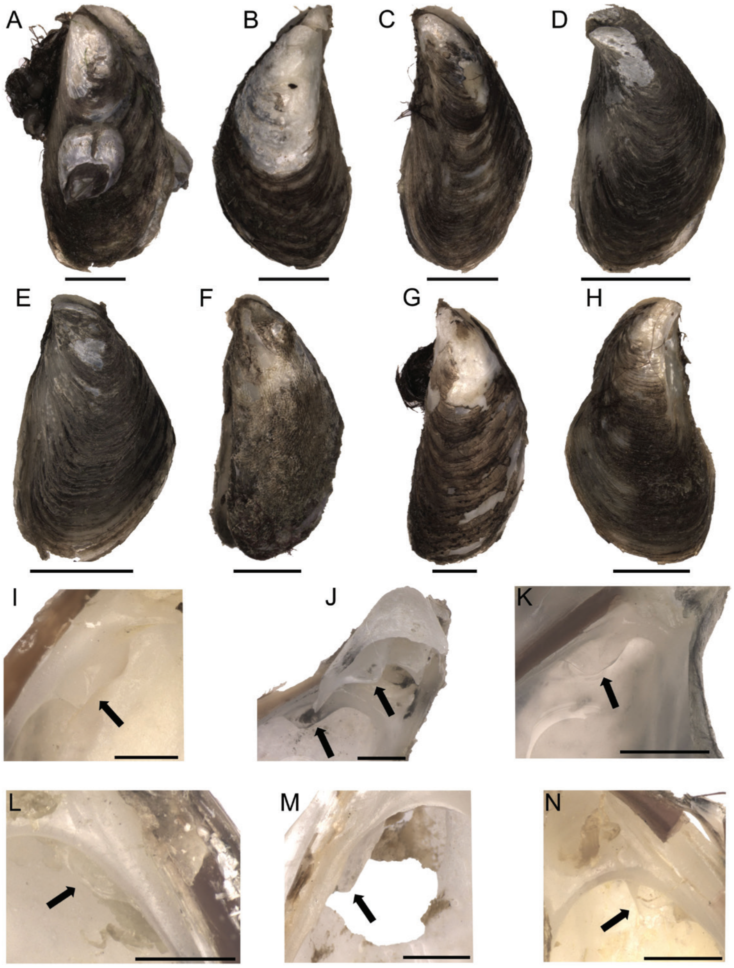

Figure 4. A-H. Specimens of *Mytilopsis leucophaeata* with DNA sequenced, from the Maricá-Guarapina lagoon system; sta. 17 (A-C), sta. 19 (D-E), sta. 21 (F-H). I-N. Apophysis (indicated by black arrows) from specimens illustrated in Figures A-B, D, F-H, respectively. Scale bars: A-H, 5 mm; I-N, 1 mm.

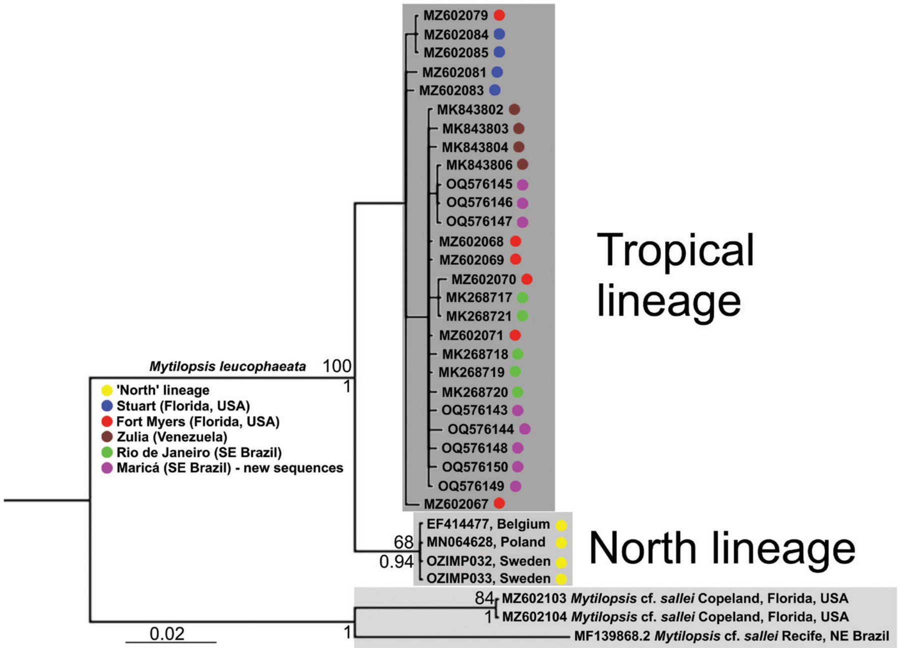

Figure 5. Tree generated by the Bayesian Inference, based on COI sequences. Bootstrap and posterior probability indexes situated respectively above and below nodes.

species, 31.7 mm (Maia-Neto et al. 2020). Shells usually had a nearly rectilinear profile (Figure 4), but some shells had a slightly curvilinear profile, broad, which is somewhat similar to the pattern of *Mytilopsis* cf. *sallei* (Fernandes et al. 2018). Juveniles of *M. leucophaeata* show a typical zigzag pattern in the shell (Fernandes et al. 2020), whereas older specimens become brownish or whitish due to the loss of the periostracum (Figure 4). The apophysis had different morphologies, such as oblong or pointed (Figure 4I-N).

The genetic investigation corroborated the identification of the eight specimens from the Maricá-Guarapina lagoon system as *M. leucophaeata* (Figure 5). Such sequences nested within the 'tropical lineage', together with the native populations from Florida (USA) and the invasive ones from South America (Venezuela and Rio de Janeiro), but apart from the 'North lineage', which shows a single COI haplotype present from NE USA, Europe and Caspian Sea (Fernandes et al. 2018, 2021).

The benthic macrofauna associated with the agglomerates of *M. leucophaeata* in the Maricá-Guarapina lagoon system was composed of 3,413 specimens belonging to seven taxa (Figure 6; Table 1): the cryptogenic *Amphibalanus improvisus* (Darwin, 1854) (Cirripedia), *Sinelobus stanfordi* (Richardson, 1901) (Tanaidacea) and *Alitta succinea* (Leuckart, 1847) (Polychaeta); and the native *Cassidinidea fluminensis* (Mañe-Garzón, 1944) (Isopoda), *Neohelice granulata* (Dana, 1851) (Brachyura), *Melita* cf. *lagunae* (Oliveira, 1953) (Amphipoda) and *Heleobia australis* (d'Orbigny, 1835) (Gastropoda).

Table 1. Abundance of the associated fauna within agglomerates of *Mytilopsis leucophaeata* at Maricá-Guarapina lagoon system, considering three replicates per station, as well as diversity (H'), equitability (J') and richness.

Species	**Sta. 14 (PVC deck)**	**Sta. 17 (sediment)**	**Sta. 21 (rocks)**
Sinelobus stanfordi	0	0	173
Amphibalanus improvisus	7	803	545
Alitta succinea	5	0	31
Heleobia australis	539	291	0
Melita cf. *lagunae*	7	84	290
Neohelice granulata	1	1	0
Cassidinidea fluminensis	1	53	25
Diversity (H')	0.2155	0.9457	1.185
Equitability (J')	0.1203	0.5876	0.7365
Richness	6	5	5

Most taxa were found in the three sampling stations (Table 1). The station 14 (PVC deck) had the highest number of associated species, however most of them with very low abundances, except *Heleobia australis*, which on the other hand was absent from station 21 (rocks). In addition to this snail, the barnacle *Amphibalanus improvisus* also showed high abundances overall, except at the station 14 (PVC deck) (Table 1; Figure 7). Only one species (*Sinelobus stanfordi*) appeared in a single station. Station 14 had the lowest diversity and equitability values, whereas station 21 had the highest values.

The highest mean density of *M. leucophaeata* was recorded at the station 14 (PVC deck), reaching 43,375 ± 46,537 specimens/m^2 (one replicate with up to 95,225 specimens/m^2), contrasting with 2,833 ± 823 specimens/m^2 and 5,925 ± 2,606 specimens/m^2 from stations 17 (soft

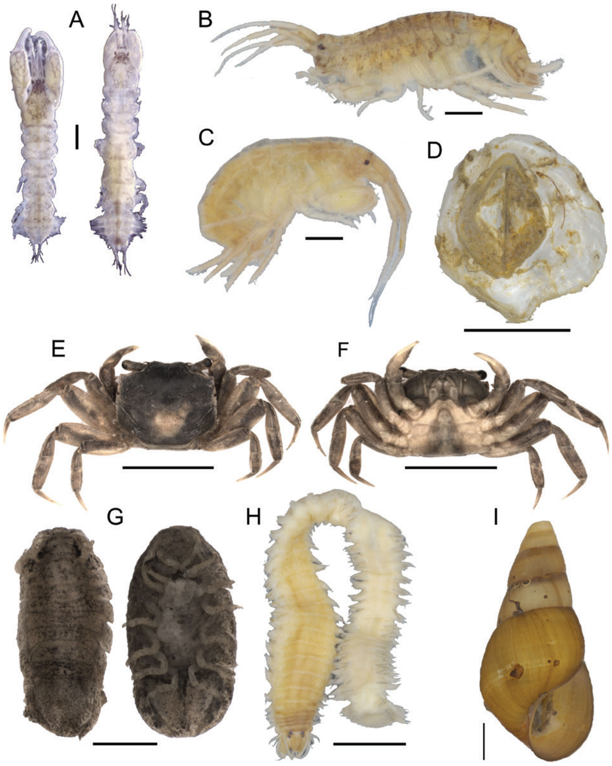

Figure 6. Benthic macrofauna associated with the agglomerates of *M. leucophaeata* in the Maricá-Guarapina lagoon system. A. *Sinelobus stanfordi*. B. *Melita* cf. *lagunae* (female). C. *Melita* cf. *lagunae* (male). D. *Amphibalanus improvisus.* E-F. *Neohelice granulata.* G. *Cassidinidea fluminensis*. H. *Alitta succinea.* I. *Heleobia australis*. Scale bars: A-C, G, I, 1 mm; D, H, 5 mm; E-F, 1 cm.

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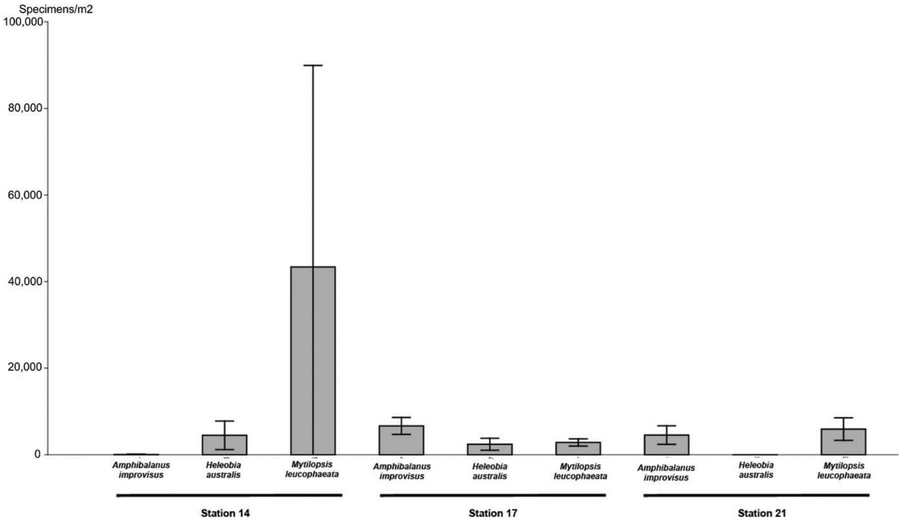

Figure 7. Density of *Mytilopsis leucophaeata, Amphibalanus improvisus* and *Heleobia australis* at the three stations in which agglomerates of the invasive bivalve were sampled in the Maricá-Guarapina lagoon system.

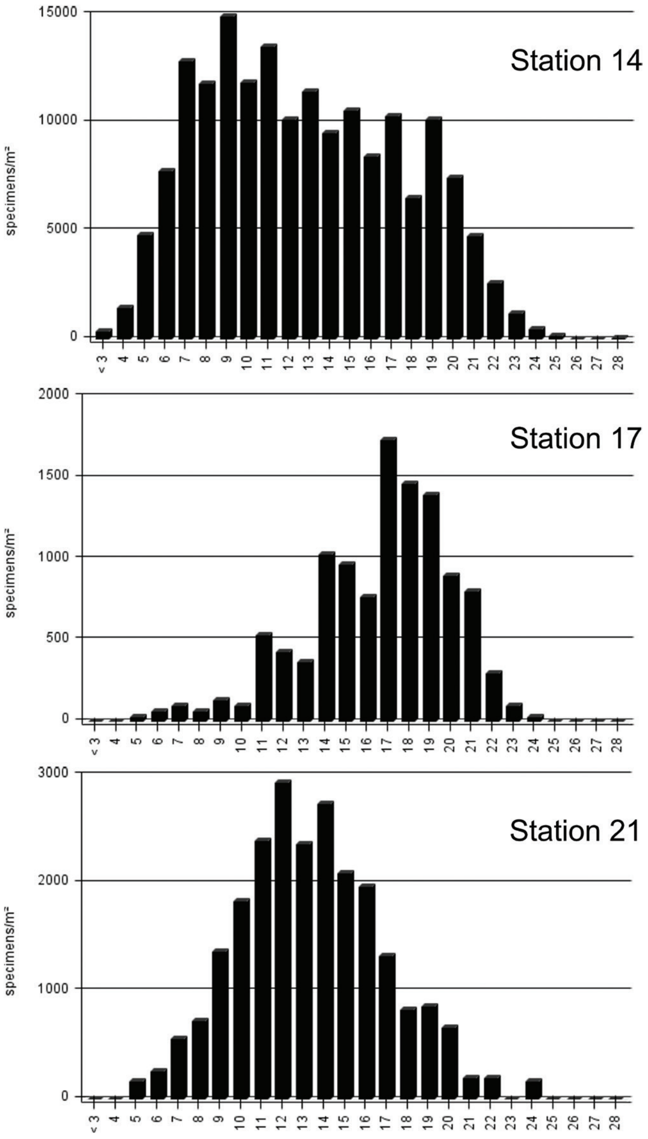

Figure 8. Density of *Mytilopsis leucophaeata* per size class (mm) at three sampling stations in the Maricá-Guarapina lagoon system.

sediment) and 21 (rocks), respectively (Figure 7). There is a large proportion of juveniles at station 14, instead of more adults and few juveniles at station 17 (Figure 8), regarding the size of 10 mm as conservative for the beginning of the reproductive stage for the 'North lineage' (Van der Gaag et al. 2020) and yet unknown for the 'tropical lineage'.

Discussion

In our studied area, some localities in the Rio de Janeiro state showed proper salinity levels for the establishment of *Mytilopsis leucophaeata*; however, this species was only found in the Maricá-Guarapina lagoon system, as a new record in addition to Rodrigo de Freitas Lagoon and Marapendi Lagoon (Rizzo et al. 2014, Fernandes et al. 2020). The measured salinities at Saquarema lagoon system and Jaconé Lagoon were respectively 7.7–20.4 and 2.2–5.4, apparently proper for the bivalve, i.e., below 18–21 ppt (Kennedy 2011, Fernandes et al. 2018, Maia-Neto et al. 2020). However, the Saquarema lagoon system may show remarkably different salinities according to the years, reaching a mean salinity of up to 33 ppt (Franco et al. 2019), which is influenced by the opening of the connection with the sea. Both estuaries do not have frequent circulation of boats from the Rio de Janeiro city (José Manoel P. Rebouças, pers. comm. – president of the Z-13 fishermen colony), especially the innermost Jaconé Lagoon. As expected, the freshwater condition of Jacarepiá Lagoon was inadequate for an introduction of *M. leucophaeata*. At the Guaratiba mangrove, the salinity varies between 27.3–29.1 ppt (Silva 2011) and 31.8–33.6 ppt (Neves et al. 2006) in the main canal and in Araçatiba, although we measured 19.9–27.4 ppt in the region (including rivers). The visited sites in Guandu River, Itaguaí and Angra dos Reis were mostly in the downstream portion of rivers, which show a higher hydrodynamics than lagoons, and might hamper the introduction of *M. leucophaeata* despite the frequent circulation of boats or even ships. In addition, salinity levels at these sampling sites were often inadequate for the bivalve (Appendix 2), and further fieldworks in more proper sites may be required.

At the Maricá-Guarapina lagoon system, there are no continuous records of salinity levels, and comparisons based on sporadic records are prone to variation in tides, seasonality, sites (e.g., close or away from rivers) and especially the opening of the main connection with the sea (Ponta Negra canal). We measured salinity levels of 16.5–17.3 ppt in Guarapina Lagoon (19 ppt in Guerra et al. 2011; 20–21 ppt in Ricevuto et al. 2013; 10–20 ppt in Laut et al. 2019), 12.9–13.8 ppt in Padres Lagoon (8 ppt in Laut et al. 2019), 10.8–13.8 ppt in Barra Lagoon (5–9 ppt in Guerra et al. 2011; 0.5–3.1 ppt in Laut et al. 2019) and 4.5–9.1 ppt in Maricá Lagoon (0 ppt in Guerra et al. 2011; 6–10 ppt in Ricevuto et al. 2013; 0.1–1 ppt in Laut et al. 2019); Franco et al. (2019) measured 8–25 ppt (winter) and 8–34 ppt (summer) in the entire lagoon system. From the recorded salinities, Guarapina Lagoon is indeed too close to the upper limit of tolerance of *M. leucophaeata*, despite considerable reductions in some events (Laut et al. 2019). The salinities measured at Padres Lagoon seem proper for the colonization of *M. leucophaeata*, as the existence of empty valves indicate such presence, but no live specimens were found. Live specimens were only found at Barra and Maricá lagoons, which showed ideal salinity levels at the sampling event, but Maricá Lagoon showed an inadequate freshwater condition in other events (Guerra et al. 2011, Laut et al. 2019). The single sampling station in the Brejo da Costa canal (a drainage canal connecting to Maricá Lagoon) had no invasive bivalves, with a reduced salinity of 2.2 ppt (Appendix 2) and few available hard substrata.

With the exceptions of stations 9 and especially 14, all other stations in Barra Lagoon showed only 0–3 live specimens of *M. leucophaeata* and hundreds of empty valves (Appendix 2). The abundance of dead specimens with articulated valves suggests the mortality events were recent. This might have been caused by sporadic openings of the Barra da Emergência canal, which was opened in 2010 and 2016 due to heavy storms, and systematically in February/March of 2019, 2020 and 2021 in order to increase the oxygen levels of the lagoon system (Maricá 2021), but also increasing salinity levels. According to local fishermen, this bivalve is common in the lagoon system since at least 2019, which might be related to the opening of this canal. There is a considerable flow of fishermen boats between the Maricá-Guarapina lagoon system and the invaded sites of *M. leucophaeata* in Rio de Janeiro city (José Manoel P. Rebouças, pers. comm.), i.e., the lagoons Marapendi and Rodrigo de Freitas, which are suggested to be the source of this secondary dispersion to the lagoon system. The distance by the sea between Rodrigo de Freitas Lagoon and Maricá Lagoon is only of ~41 km (Barra da Emergência canal) and ~53 km (Ponta Negra canal), which are covered in a few hours by a small boat.

The artificial substrate at station 14 (a mobile PVC deck) had by far the highest abundance of *M. leucophaeata* in the lagoon system (Figure 7). According to the Maricá prefecture (pers. comm.), this structure is used during studies of water quality in the region; however, we could not obtain records of when the deck was settled and whether it was allocated in other sites of the lagoon system (or outside of it). This high abundance confirms the preference of this species for hard and wide surfaces situated considerably far from the sediment; because they are filter feeders, the proximity with the soft sediment may be harmful (Fernandes et al. 2020). Station 14 showed a large proportion of juveniles (Figure 8), which indicate that the gregarious behavior of larvae are still acting even in such dense agglomerates. The scarce abundances of the associated species in this station (except by the snail *H. australis*) and the consequent reduced diversity/equitability raise suspicious whether the PVC deck was recently moved and colonized by the associated fauna. The agglomerates of *M. leucophaeata* in the soft sediment of Maricá Lagoon were sparse and did not form a reef, such as observed in Marapendi Lagoon (Fernandes et al. 2020); the bivalves at station 17 were mainly adults, with few cohorts of juveniles, suggesting these agglomerates may not prosper in this inadequate habitat.

Another factor that may influence the local density of *M. leucophaeata* in the Maricá-Guarapina lagoon system is organic pollution, which is considered high or much high in the estuary and rivers that discharge in it (INEA 2021b; using data from 2012–2021). For example, we are unaware whether the scarcity or even absence of live specimens of *M. leucophaeata* at stations 20 and 22 were caused by excessive pollution (the former situated near a sewage exit, the latter at the mouth of a polluted river), or whether the availability of hard substrata in both sites is too recent for the colonization of *M. leucophaeata*.

The fauna associated to the agglomerates of *M. leucophaeata* in the Maricá-Guarapina lagoon system is similar to those obtained in the agglomerates from Marapendi and Rodrigo de Freitas lagoons (Fernandes et al. 2020, Rodrigues et al. 2021), with the shared presence of *Alitta succinea*, *Amphibalanus improvisus*, *Melita* spp. and *Heleobia* spp. The mud crab *Eurypanopeus dissimilis* (Benedict & Rathbun, 1891) identified from these two estuaries was absent from the agglomerates in Maricá-Guarapina, which otherwise housed two specimens of *Neohelice granulata*. Similarly to Marapendi Lagoon and contrary to Rodrigo de Freitas Lagoon, there were no native mussels *Brachidontes darwinianus* (d'Orbigny, 1842) in Maricá-Guarapina. Similarly to Rodrigo de Freitas Lagoon and contrary to Marapendi Lagoon, there were no shell-boring polychaetes *Polydora* sp. in the agglomerates from Maricá-Guarapina, but there were *Cassidinidea fluminensis* and *Sinelobus stanfordi*.

Together with the proper salinity gradient, the anthropic pressure at Maricá-Guarapina is the main cause for the well-succeeded invasion of *M. leucophaeata* there due to the environmental fragility and reduced biological competition in this estuary, adequate for new invasions. The constant investigation about the expansion range of invasive species and their interactions with the local fauna is essential to understand the impacts in the ecosystem. More rigor in the surveillance of invasive species and a better interlocution between public, private and nonprofit agencies are required.

Supplementary Material

The following online material is available for this article:
Appendix 1.
Appendix 2.

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Author Contribution

Clarisse Duarte da Rocha: conducted the fieldworks; sorted, counted and photographed the specimens at laboratory; created figures and drafted the initial version of the manuscript; contributed to the final version of the manuscript.

Maurício Romulo Fernandes: designed the project; conducted the fieldworks; sorted, counted and photographed the specimens at laboratory; performed the genetic procedures; created figures and drafted the initial version of the manuscript; contributed to the final version of the manuscript.

Igor Christo Miyahira: designed the project; conducted the fieldworks; created maps (Figures 1–2); provided financial support; contributed to the final version of the manuscript.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data availability

DNA sequences are stored in the GenBank database under codes OQ576143-OQ576150. The fauna associated to 'sururu' (*Mytella strigata*) mussels in Guaratiba (Appendix 1) and data related to fieldwork (Appendix 2) are available at the Biota Neotropica Dataverse, respectively under the links: https://doi.org/10.48331/scielodata.9UCE2U and https://doi.org/10.48331/scielodata.USSCCU.

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Inventory

Fish fauna of the São Francisco River Interbasin Water Transfer reservoirs

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GUTIERRE, S.M.M., SILVA, A.L.B., GALVÃO, G.A., SILVA, L.R.A., PEREIRA, L.C.M., NICOLA, P.A. **Fish fauna of the São Francisco River Interbasin Water Transfer reservoirs**. Biota Neotropica 23(3): e20231499. https://doi.org/10.1590/1676-0611-BN-2023-1499

Abstract: Artificial impoundments are frequently built to mitigate the water scarcity in the drylands such as the Caatinga region in Brazil. The São Francisco Interbasin Water Transfer (SF-IWT) megaproject implemented many artificial reservoirs for that purpose. A checklist of fish species from the SF-IWT reservoirs is provided based on samples from eight years of monitoring. The collections were conducted semiannually at 28 reservoirs divided into three groups: the East Axis, North Axis, and Agreste Branch. The SF-IWT reservoirs presented a total of 47 species, 46 were recorded in the North Axis, 27 in the East Axis, and only seven in the Agreste Branch. Characids and cichlids represented most of the species. The three analyzed groups of reservoirs presented distinct communities and the reservoirs' age, richness and abundance were relevant variables responsible for fish composition. The SF-IWT reservoirs present a diverse and heterogeneous ichthyofauna, typical of lentic environments. The main colonizers of the SF-IWT reservoirs were fish from the São Francisco donor basin, invasive species anthropically released in those sites, and eventual species from the surrounding receiving basins. As the accumulation curves suggested, a continuous effort could reveal additional species, patterns in long-term colonization, and contribute to data on the reservoirs' future stabilization phase. Since invasive species were present in most reservoirs, along with donor-basin native species with potential to disperse to the receiving basins, a continuous and detailed monitoring is key for management planning and possible impacts assessment.

Keywords: *Artificial reservoirs; Brazilian Semiarid; non-native fish; water diversion.*

Ictiofauna dos reservatórios do Projeto de Integração do Rio São Francisco

Resumo: Barramentos artificiais são comumente construídos para mitigar a escassez hídrica em áreas semiáridas como a região da Caatinga brasileira. O Projeto de Integração do Rio São Francisco (PISF) com Bacias Hidrográficas do Nordeste Setentrional implementou muitos reservatórios artificiais com este propósito. Uma lista de espécies de peixes dos reservatórios do PISF foi obtida após amostragens realizadas em oito anos de monitoramento. As campanhas foram realizadas semestralmente em 28 reservatórios divididos em três grupos: Eixo Leste, Eixo Norte e Ramal do Agreste. Os reservatórios amostrados apresentaram um total de 47 espécies, 46 delas foram registradas no Eixo Norte, 27 no Eixo Leste e apenas sete no Ramal do Agreste. Characidae e Cichlidae foram as famílias mais representativas. Os três grupos de reservatórios analisados apresentaram comunidades distintas e a idade, a riqueza e a abundância de cada reservatório foram as variáveis que mais influenciaram a composição das espécies de peixes. Os reservatórios do PISF apresentaram uma ictiofauna diversa e heterogênea, característica de ambientes lênticos. Os principais colonizadores dos reservatórios do PISF foram peixes da bacia doadora do São Francisco, espécies invasoras antropicamente liberadas nesses locais e eventuais espécies das bacias receptoras do entorno. De acordo com o resultado das curvas de acúmulo, um esforço contínuo poderia revelar espécies adicionais, padrões na colonização em longo prazo e contribuir com dados para a fase futura de estabilização dos reservatórios. Visto que espécies invasoras estiveram presentes em quase todos os reservatórios, juntamente com espécies nativas da bacia doadora com potencial de dispersão para as bacias receptoras, um monitoramento continuo e detalhado é essencial para o planejamento de manejo e avaliação de impactos.

Palavras-chave: *Desvio de águas; Peixes não-nativos; Reservatórios artificiais; Semiárido brasileiro.*

Introduction

The Semiarid Northeast region of Brazil, dominated by the Caatinga biome, has very low precipitation ranging from 200 mm to 800 mm annually, with short rainy periods of two to four months (January to April), and a long dry period (generally from May to December) (Maltchik 1999). The average annual temperature ranges from 25 to 30° C, with the maximum reaching almost 40° C in hotter months (September to November). These two distinct seasons in the Caatinga, wet and dry with extremely low precipitation, are responsible for the great number of intermittent rivers (Maltchik & Florín 2002). The deficit in the hydric balance has a major socioeconomic impact in semi-arid regions, leaning policymakers to focus on solutions that minimize social issues and meet economic needs. The implementation of artificial man-made reservoirs is reported as a commonly used way to mitigate the water scarcity in dry regions, supplying water for both economic (e.g., irrigation, agriculture, industry) and domestic use (Thornton & Rast 1993).

In the Brazilian semi-arid, the São Francisco Interbasin Water Transfer (SF-IWT) project was the governmental solution to mitigate centuries of water scarcity (Andrade et al. 2011). The São Francisco River, the largest exclusively Brazilian river, is the main naturally perennial water resource in the Semiarid Caatinga domain (Andrade et al. 2011, Roman 2017) and, therefore, the groundwork for the SF-IWT. The SF-IWT megaproject consists of 477 km of canals, pipes, aqueducts, pump stations, and reservoirs divided into two main axes: East (EA) and North (NA) (Andrade et al. 2011), diverting water from the donor basin (São Francisco) to eight different receiving basins. By August 2022, 12 of the SF-IWT artificial reservoirs along the EA and 14 along the NA were fully operational. Moreover, the EA sub-division, the Agreste branch (AB), possesses two more fully operational reservoirs. The EA axis provides water to the receiving basins of the Paraíba do Norte, Moxotó, and Pajeú rivers, and its AB to the Ipojuca River basin, located in a region known as "Agreste". Meanwhile, the NA axis supplies water to receiving basins of the Jaguaribe, Apodi-Mossoró, Piranhas-Açu, and Brígida rivers (Andrade et al. 2011).

The SF-IWT reservoirs are artificially regulated, receiving water from the perennial Sao Francisco River according to management demands, not following the natural seasonal variation affected by the longer dry and shorter rainy periods. Furthermore, due to these man-regulated dynamics, the SF-IWT reservoirs present distinctive features from other semi-arid reservoirs (Barbosa et al. 2012, Barbosa et al. 2021). For the same reason, the fish fauna in the SF-IWT reservoirs is directly affected by the water management dynamics. Silva et al. (2020) compiled information on the ichthyofauna of five basins surrounding the SF-IWT, generating a comprehensive baseline of that Semiarid region previous to the project's full implementation. Meanwhile, Silva et al. (2023) analyzed the fish fauna that is dispersing through the SF-IWT East Axis reaching the Paraíba do Norte River receiving basin after ten years of water diversion. Nonetheless, previous studies did not discuss the fish taxonomic composition of artificially created SF-IWT reservoirs. Thus, this work aimed to provide a list of fish species recorded in the 28 SF-IWT artificial reservoirs, and the results represent important insights on the changes in the fish community composition that occurred over the eight years of monitoring.

Material and Methods

1. *Sampling area*

Field campaigns were conducted twice a year, from 2015 to 2022, in 12 reservoirs of the SF-IWT East Axis (EA), 14 reservoirs in the North Axis (NA), and two reservoirs in its Agreste branch (AB) (Figure 1). All the reservoirs on the East Axis and the Agreste Branch, in addition to

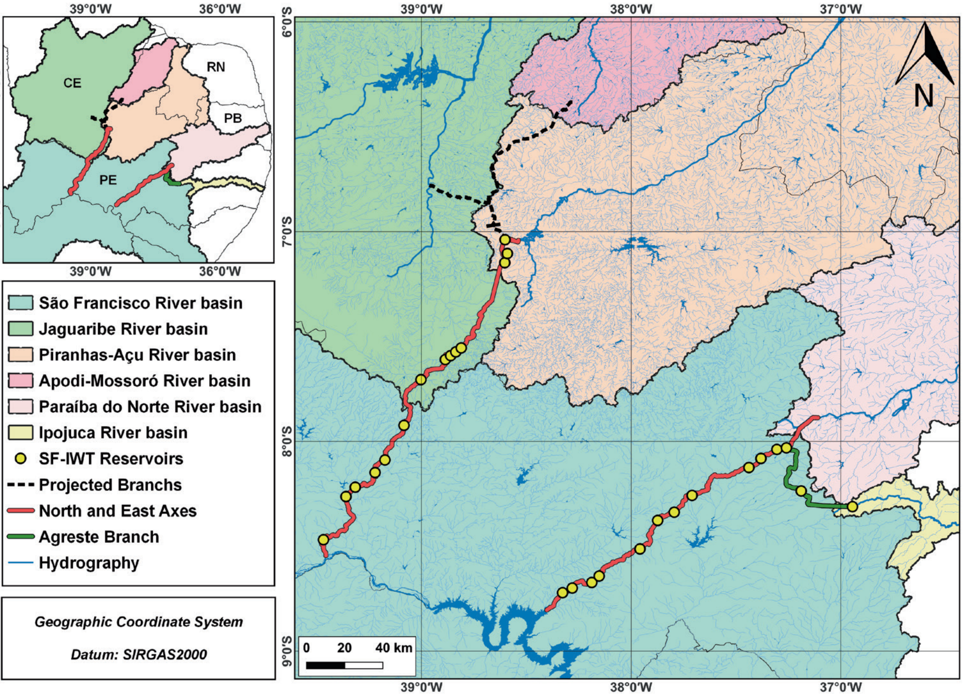

Figure 1. Study area showing the 28 São Francisco Interbasin Water Transfer reservoirs, the São Francisco River, and the basins surrounding the transposition project.

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six reservoirs on the North Axis are located in the state of Pernambuco, Brazil; five reservoirs of the North Axis are located in the state of Ceará, and three in the state of Paraíba, Brazil. Despite being a sub-section of the EA, the AB was separately considered since it diverts the SF-IWT waters to the Ipojuca River basin, while EA diverts to the Paraíba do Norte River basin. The branch is also located in a unique region of the Caatinga, the Agreste, a transition area between the forest (humid sub-region with tropical vegetation) and the semiarid (a dry sub-region with semi-arid vegetation) (CONDEPE 2005).

2. *Sampling effort*

A three-days-sampling effort was conducted for each analyzed reservoir. Each three-days-sampling corresponded to one campaign. Campaign numbers varied for each sampling site since the reservoirs presented different filling dates (Table 1), according to the SF-IWT construction progress. Fish were caught using trawls (10 m long, 5 mm mesh), sieves (50 cm diameter, 5 mm mesh), cast nets (mesh sizes of 15 and 30 mm between opposite knots), and hand nets (40 cm/side rectangular base, 5 mm mesh), with at least three attempts per sampling-day for each of those methods. Gill nets (10 or 50 m long with mesh sizes of 20, 30, 40, 50, 60, and 80 mm between adjacent knots) were kept for one sampling-night (12–14 hours) at each site. In eventual encounters with fisherman during sampling, we registered the species collected by them and added to our data as one record (one specimen per species).

3. *Processing of collected specimens*

Captured fish were promptly identified and released. When identification was not possible in the field, specimens were euthanized by overexposure to 1 g/mL clove oil (based on MCTI – CONCEA 2018), fixed in a 10% formaldehyde solution, preserved in 70° GL alcohol, and transported to be identified in the Laboratório de Ictiologia (CEMAFAUNA, Universidade Federal do Vale do São Francisco – UNIVASF). Voucher specimens were deposited in the Ichthyological Collection of the Museu de Fauna da Caatinga (MFCI), UNIVASF, Petrolina, Brazil. The material was registered in the SisGen (Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado) system, under the license number A8EC2B0. Fish species were identified according to identification keys provided by Britski et al. (1988) and Ramos et al. (2018), original species descriptions, and complemented by reviews of some taxonomic groups. The nomenclature and systematic classification of species were based on Betancur-R et al. (2017) and Fricke et al. (2023).

4. *Data analysis*

The richness extrapolation estimator (Chao, 2005) was calculated and the generated accumulation curve (EstimateS v9.1.0) was used to demonstrate the fish sampling efficiency. We used Chao1 and Chao2 estimators combined to verify whether the estimates were dependent on sample size or stabilized towards the full sampling. The reservoirs' age (months since filling date), each axis or branch (East, North, Agreste), fish abundance, and richness were used as explanatory variables to assess the relevance of the independent variables (reservoirs). The most suitable model was generated using an ordistep information criterion. The ordistep builds a forward model so that it maximizes the adjusted R2 at every step, and stops when the adjusted R2 starts to decrease, the scope is exceeded, or the selected permutation P-value is exceeded (Blanchet et al. 2008). The model analysis is used to identify predictor variables that significantly explain the patterns observed in the fish assemblage. Furthermore, a db-RDA (Distance-based Redundancy Analysis) was performed to visualize dbLM data, and a PERMANOVA based on the similarity matrix obtained by Euclidean distance, with 999 permutations, helped determine the significance of explanatory variables. Statistical analysis, other than richness estimators, was

Table 1. A detailed list of names and locations of the 28 artificial reservoirs of São Francisco Interbasin Water Transfer Project. Reservoirs are ordered according to the Axis (North, East, or Agreste Branch), and distance from the São Francisco River (closer to farthest). Each reservoir was filled on different dates, according to the construction progress, and the number of campaigns (one campaign = 3-day-sampling, bi-annual) was counted after filling date.

Reservoir	Latitude	Longitude	Filling Date	Campaigns
North Axis (NA)				
Tucutu	08°28'09"S	39°27'57"W	Jul-2015	14
Terra Nova	08°15'49"S	39°21'18"W	Dec-2015	12
Serra do Livramento	08°13'09"S	39°18'59"W	Dec-2017	7
Mangueira	08°08'41"S	39°13'08"W	Apr-2018	8
Negreiros	08°05'25"S	39°10'48"W	Aug-2018	3
Milagres	07°55'02"S	39°04'40"W	Jan-2020	4
Jati	07°42'33"S	39°00'21"W	Jun-2020	4
Porcos	07°37'43"S	38°53'19"W	Jan-2021	2
Cana Brava	07°35'18"S	38°51'18"W	Jul-2022	1
Cipó	07°34'29"S	38°50'36"W	Aug-2022	1
Boi	07°33'40"S	38°49'09"W	Sep-2022	1
Morros	07°09'07"S	38°36'21"W	Oct-2021	1
Boa Vista	07°06'09"S	38°35'35"W	Oct-2021	1
Caiçara	07°02'04"S	38°36'09"W	Jan-2022	2
East Axis (EA)				
Areias	08°43'13"S	38°19'17"W	Oct-2014	16
Braúnas	08°41'43"S	38°16'44"W	Oct-2015	8
Mandantes	08°40'18"S	38°11'13"W	Jan-2017	5
Salgueiro	08°38'39"S	38°09'08"W	Jan-2017	5
Muquem	08°30'54"S	37°57'24"W	Feb-2017	11
Cacimba Nova	08°21'43"S	37°51'53"W	Feb-2017	5
Bagres	08°20'07"S	37°47'35"W	Feb-2017	5
Copiti	08°15'26"S	37°42'31"W	Feb-2017	11
Moxotó	08°07'26"S	37°26'14"W	Feb-2017	4
Barreiro	08°04'43"S	37°22'33"W	Feb-2017	4
Campos	08°02'10"S	37°18'26"W	Mar-2017	4
Barro Branco	08°01'52"S	37°15'38"W	Mar-2017	11
Agreste Branch (AB)				
dos Góis	08°13'40"S	37°10'48"W	Feb-2021	6
Ipojuca	08°18'41"S	36°56'40"W	Dec-2021	6

performed using R software (R Core Team, 2020). The functions used were from package Vegan (Oksanen et al. 2013). Plots were made using the package ggplot2 (Wickham, 2006).

Results

A total of 70,522 individuals representing 47 fish species (Figures 2 and 3) from 18 families, and seven orders were registered (Table 2). The North Axis (NA) presented 46 species, 27 species were registered in the East Axis (EA), and seven in the Agreste Branch (AB). There was one exclusive species from the AB reservoirs (*Parotocinclus jumbo* Britski & Garavello, 2002), and 20 species were only registered in the NA reservoirs (see Table 2). *Anchoviella vaillanti* (Steindachner, 1908), *Astyanax lacustris* (Lütken, 1875), *Oreochromis niloticus* (Linnaeus, 1758), and *Poecilia reticulata* Peters, 1859 were the only common species to all three analyzed groups of reservoirs (Figures 2 and 3). The richest order was Characiformes (59.5%; n = 28), followed by Cichliformes (14.9%; n = 7), and Siluriformes (10.6%; n = 5). The fish families with greater species richness were Characidae (25.5%; n = 12), and Cichlidae (14.8%; n = 7). Eight fish were considered non-native to the Caatinga domain, while eight are endemic in the region (Table 2).

Table 2. Fish species collected in the East and North Axis and the Agreste Branch reservoirs of the São Francisco Interbasin Water Transfer Project. Status: N = Native to the Caatinga domain, NN = Non-Native to the Caatinga domain, E = Endemic to the Caatinga domain. Origin: DB = Donor Basin (São Francisco River basin), WS = Wide Spread in the Caatinga and other Brazilian regions, AM = Amazon River basin, AF = Africa, CA = Central America.

Taxa	Abundance			Status	Origin	Voucher
	EA	NA	AB			
CLUPEIFORMES						
Engraulidae						
Anchoviella vaillanti (Steindachner, 1908)	9303	8220	303	N	DB*	MFCI009548
CHARACIFORMES						
Erythrinidae						
Hoplias gr. *malabaricus* (Bloch, 1794)	166	218	0	N	WS	MFCI009030
Serrasalmidae						
Metynnis lippincottianus (Cope, 1870)	361	645	0	NN	AM	MFCI007745
Myleus micans (Lütken, 1875)	1	115	0	N	DB	MFCI006078
Pygocentrus piraya (Cuvier, 1819)	0	4	0	N	DB	MFCI007335
Serrasalmus brandtii Lütken, 1875	809	801	0	N	WS	MFCI006616
Anostomidae						
Leporinus piau Fowler, 1941	0	84	0	N	WS	MFCI009274
Leporinus taeniatus Lütken, 1875	1	2	0	E	WS	MFCI006142
Megaleporinus obtusidens (Valenciennes, 1836)	0	1	0	N	DB**	MFCI009276
Schizodon knerii (Steindachner, 1875)	0	3	0	E	DB	Not Deposited
Curimatidae						
Steindachnerina elegans (Steindachner, 1875)	0	70	0	N	DB	MFCI008967
Steindachnerina notonota (Miranda Ribeiro, 1937)	0	9	0	E	WS	Not Deposited
Prochilodontidae						
Prochilodus brevis Steindachner, 1875	0	5	0	E	WS	Not Deposited
Triportheidae						
Triportheus guentheri (Garman, 1890)	5	11	0	E	DB	MFCI006639
Iguanodectidae						
Bryconops aff. *affinis* (Günther, 1864)	248	1018	0	N	DB	MFCI007135
Acestrorhynchidae						
Acestrorhynchus britskii Menezes, 1969	0	3	0	N	DB	MFCI008954
Acestrorhynchus lacustris (Lütken, 1875)	4	20	0	N	DB	MFCI008600
Characidae						
Astyanax lacustris (Lütken, 1875)	10355	11411	496	N	WS	MFCI006038
Compsura heterura Eigenmann, 1915	0	9	0	N	WS	Not Deposited

Continue...

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Taxa	**Abundance**			**Status**	**Origin**	**Voucher**
	EA	**NA**	**AB**			
Hemigrammus brevis Ellis, 1911	1033	1319	0	N	DB	MFCI009773
Hemigrammus gracilis (Lütken, 1875)	59	2026	0	N	DB	MFCI005989
Hemigrammus marginatus Ellis, 1911	1200	3236	0	N	WS	MFCI007328
Moenkhausia costae (Steindachner, 1907)	4732	515	0	E	WS*	MFCI006632
Phenacogaster franciscoensis Eigenmann, 1911	0	53	0	N	DB	MFCI007724
Psalidodon fasciatus (Cuvier, 1819)	0	670	0	N	WS	MFCI009546
Psellogrammus kennedyi (Eigenmann, 1903)	0	84	0	N	WS	MFCI008975
Roeboides xenodon (Reinhardt, 1851)	238	373	0	N	DB	MFCI006104
Serrapinnus heterodon (Eigenmann, 1915)	0	183	0	N	WS	MFCI007800
Serrapinnus piaba (Lütken, 1875)	0	15	0	N	WS	MFCI006614
GYMNOTIFORMES						
Sternopygidae						
Sternopygus macrurus (Bloch & Schneider, 1801)	3	10	0	N	DB	MFCI007342
SILURIFORMES						
Callichthyidae						
Hoplosternum littorale (Hancock, 1828)	1	39	0	NN	WS	MFCI008654
Loricariidae						
Hypostomus pusarum (Starks, 1913)	24	24	0	E	WS	MFCI006141
Parotocinclus jumbo Britski & Garavello, 2002	0	0	10	E	WS	MFCI008769
Auchenipteridae						
Trachelyopterus galeatus (Linnaeus, 1766)	379	159	0	N	WS	MFCI006178
Pimelodidae						
Pimelodus maculatus Lacepède, 1803	0	2	0	N	DB	Not Deposited
CICHLIFORMES						
Cichlidae						
Cichla monoculus Spix & Agassiz, 1831	970	1217	3	NN	AM	MFCI006070
Cichla temensis Humboldt, 1821	0	143	0	NN	AM	Not Deposited
Cichlasoma orientale Kullander, 1983	2	21	0	N	WS	MFCI008668
Cichlasoma sanctifranciscense Kullander, 1983	452	160	0	N	DB**	MFCI007165
Oreochromis niloticus (Linnaeus, 1758)	2866	1245	872	NN	AF	MFCI009495
Parachromis managuensis (Günther, 1867)	0	2	373	NN	CA	MFCI008759
Saxatilia brasiliensis (Bloch, 1792)	1	124	0	N	WS	MFCI009495
CYPRINODONTIFORMES						
Poeciliidae						
Poecilia hollandi (Henn, 1916)	338	190	0	N	DB	MFCI009035
Poecilia reticulata Peters, 1859	95	14	183	NN	AM	MFCI007303
Poecilia vivipara Bloch & Schneider, 1801	1441	522	0	N	WS	MFCI006752
ACANTHURIFORMES						
Sciaenidae						
Pachyurus francisci (Cuvier, 1830)	0	67	0	N	DB	MFCI006591
Plagioscion squamosissimus (Heckel, 1840)	2	362	0	NN	AM	MFCI006081

* Introduced in the East Axis receiving basin, Paraíba do Norte (Ramos et al. 2021; Silva et al. 2023). ** Reports in the receiving basins, Paraíba do Norte and Jaguaribe (in prep.)

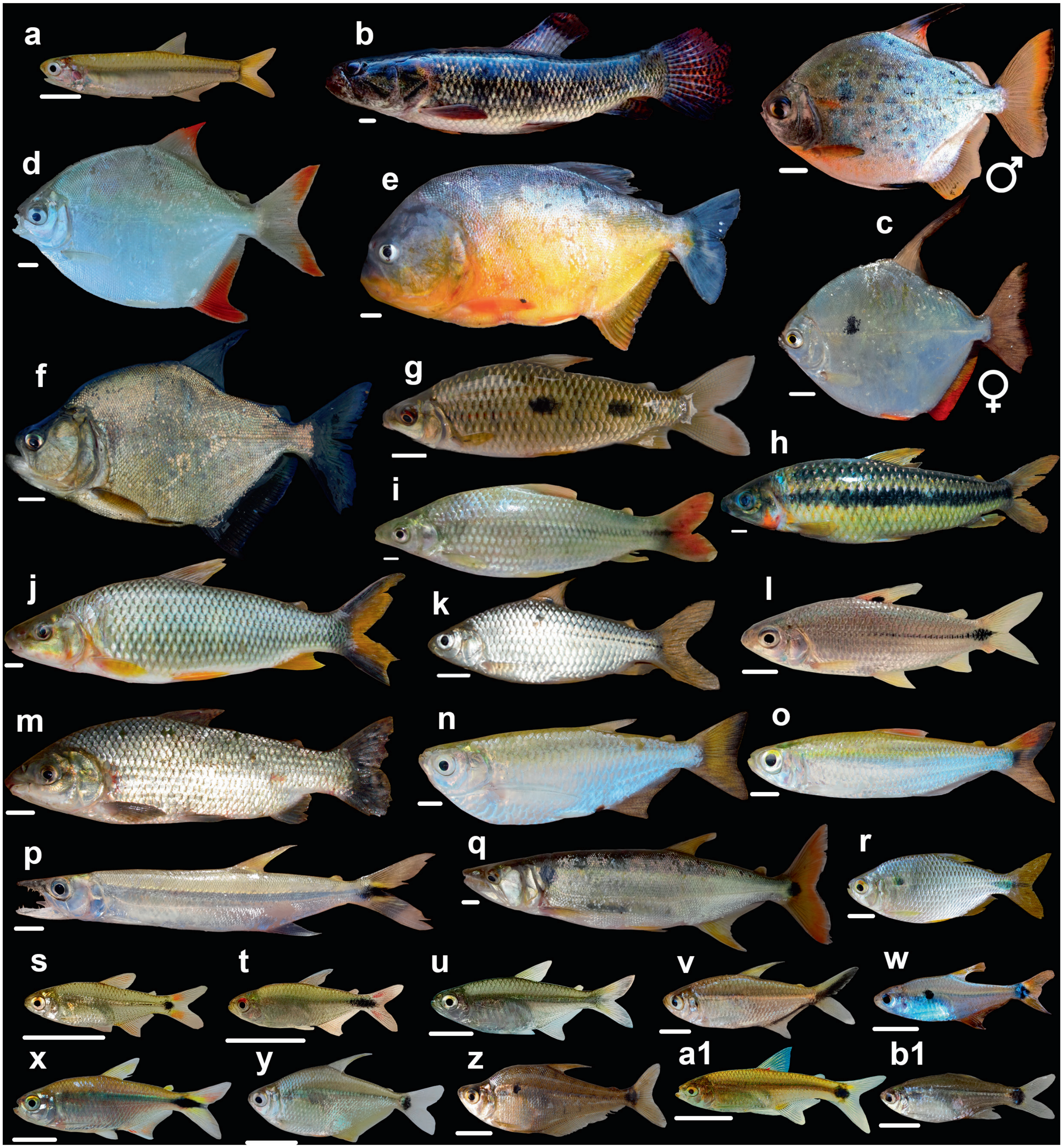

Figure 2. Clupeiformes and Characiformes collected in in the São Francisco Interbasin Water Transfer reservoirs: a. *Anchoviella vaillanti,* b. *Hoplias* gr. *malabaricus,* c. *Metynnis lippincottianus*, d. *Myleus micans*, e. *Pygocentrus piraya*, f. *Serrasalmus brandtii*, g. *Leporinus piau*, h. *Leporinus taeniatus*, i. *Megaleporinus obtusidens*, j. *Schizodon knerii*, k. *Steindachnerina elegans*, l. *Steindachnerina notonota*, m. *Prochilodus brevis*, n. *Triportheus guentheri*, o. *Bryconops* aff. *affinis*, p. *Acestrorhynchus britskii*, q. *Acestrorhynchus lacustris*, r. *Astyanax lacustris*, s. *Compsura heterura*, t. *Hemigrammus brevis*, u. *Hemigrammus marginatus*, v. *Moenkhausia costae*, w. *Phenacogaster franciscoensis*, x. *Psalidodon fasciatus*, y. *Psellogrammus kennedyi*, z. *Roeboides xenodon*, a1. *Serrapinnus heterodon,* and b1. *Serrapinnus piaba*. Scale bar = 1 cm.

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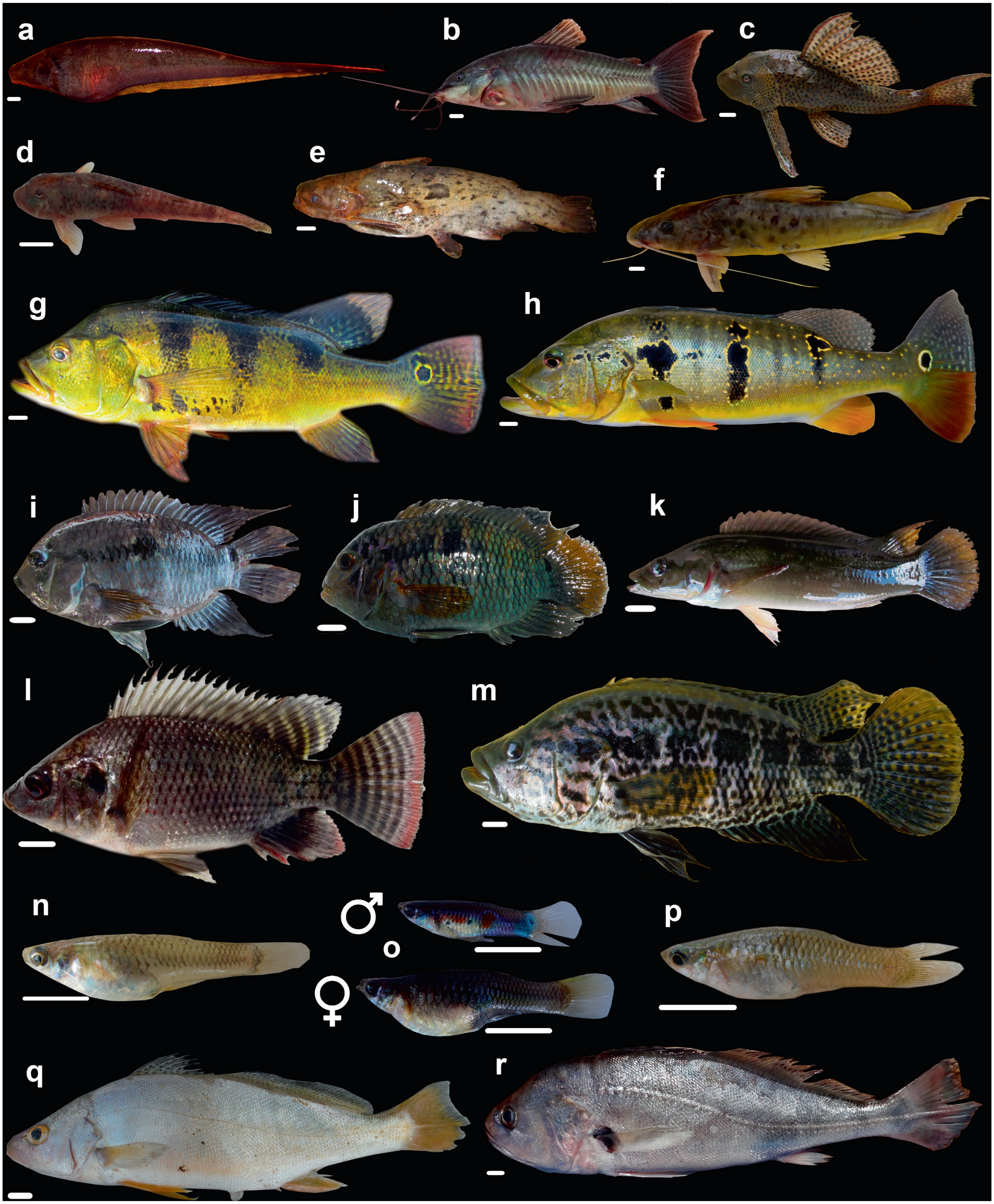

Figure 3. Gymnotiformes, Siluriformes, Cichliformes, Cyprinodontiformes, and Acanthuriformes collected in the São Francisco Interbasin Water Transfer reservoirs: a. *Sternopygus macrurus*, b. *Hoplosternum littorale*, c. *Hypostomus pusarum*, d. *Parotocinclus jumbo*, e. *Trachelyopterus galeatus*, f. *Pimelodus maculatus*, g. *Cichla monoculus*, h. *Cichla temensis*, i. *Cichlasoma orientale*, j. *Cichlasoma sanctifranciscense*, k. *Saxatilia brasiliensis*, l. *Oreochromis niloticus*, m. *Parachromis managuensis*, n. *Poecilia hollandi*, o. *Poecilia reticulata*, p. *Poecilia vivipara*, q. *Pachyurus francisci*, and r. *Plagioscion squamosissimus*. Scale bar = 1 cm.

The most abundant species in the EA reservoirs were *As. lacustris* (30%), *A. vaillanti* (27%), *M. costae* (14%), and *O. niloticus* (8%). In NA reservoirs, the predominant species were *As. lacustris* (34%), *A. vaillanti* (22%), and *Hemigrammus marginatus* (9%). Meanwhile, in AB the species with the largest number of individuals were *O. niloticus* (47%), *As. lacustris* (22%), and *Parachromis managuensis* (17%). In general, the most predominant species were *As. lacustris* (32%), *A. vaillanti* (24%), and *M. costae* (8%) (Figures 2 and Figure 3).

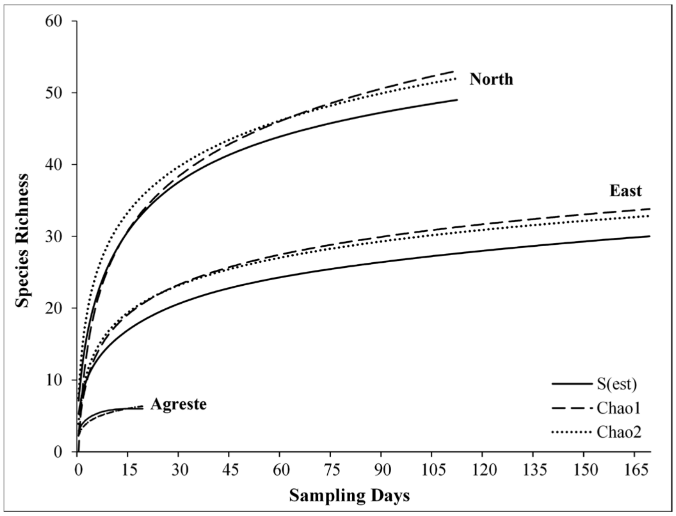

Figure 4. Species accumulation curve with expected number of species – S(est) – and the richness extrapolation estimators Chao 1 (abundance-based data) and Chao 2 (incidence-based data). Sample collections made in the three group of reservoirs from the São Francisco Interbasin Water Transfer project: East Axis, North Axis, Agreste Branch.

Table 3. Forward selection model ANOVA with adjusted p-testing for significant variables between fish assemblage (abundance, richness) and reservoir characteristics (age, axis). * Significance at $p < 0.05$; Df = degrees of freedom; AIC = Akaike Information Criterion.

ANOVA	Df	Adjusted R2	AIC	F	Pr(>F)
Abundance	1	0.282	148.36	11.630	**0.002***
Age	1	0.273	141.79	1.547	**0.042***
Axis	2	0.145	143.73	4.330	**0.002***
Richness	1	0.269	141.43	3.819	**0.002***

During the first years of sampling in the reservoirs, the same species were recurrent recorded in most of them: *A. vaillanti*, *As. lacustris*, *H. malabaricus, M. costae*, and *O. niloticus* (Supplementary File S1).

Data suggests that increasing the sampling effort would result in collecting additional species since the species accumulation curves did not present a tendency to stabilize, except for the Agreste Branch (Figure 4). The richness estimators indicated that the East Axis would present additional six species (observed n = 27), and seven in the North Axis (observed n = 46).

The forward selection model applied to fish assemblage (abundance, richness) and reservoir (age, location) characteristics (Figure 1, Table 1) identified richness, abundance, age, and location (Axis) as good predictors (Table 3). The first db-RDA axis (CAP 33.1%) distinguished reservoirs location and age (Figure 5). The second db-RDA axis was related to reservoir richness and abundance, explaining 16.5% of the variation in fish composition. Areias (EA) and Tucutu (NA) reservoirs are represented in the farther left of CAP1 since those were the reservoirs most influenced by richness and abundance.

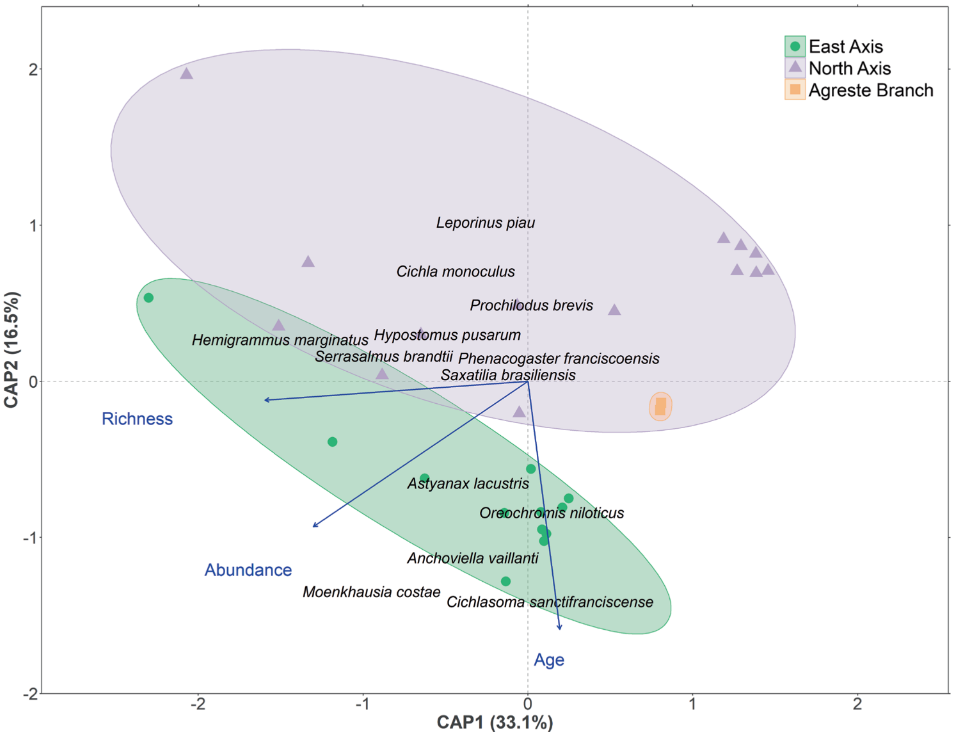

Figure 5. Ordination of 28 reservoirs in the São Francisco Interbasin Water Transfer project according to the distance-based redundancy analysis (db-RDA), with the effect of reservoir age on fish assemblages. Represented species are the most strongly related to the ordination axes: R2 > 0.5.

Discussion

The São Francisco Interbasin Water Transfer artificial reservoirs presented 47 fish species, the great majority represented in the North Axis, about half of them were presented in the East Axis, and only seven were found in the Agreste Branch. Characids and cichlids represented most of the reported species. The three analyzed groups of reservoirs presented distinct fish compositions, however, AB shared most species with both axes. The reservoirs' richness, abundance, and age were relevant variables responsible for fish composition, separating axes and species groups. The species that first colonized the reservoirs and recurrently occurred in fist years of sampling, considered as pioneer species, were: *A. vaillanti*, *As. lacustris*, *O. niloticus*, *M. costae*, and *H. malabaricus*.

All the SF-IWT reservoirs are less than ten years old, still in the colonization formation stage (Agostinho et al. 1999). The instability of reservoir conditions can last 5 to 30 years after its formation, with fish community stabilization estimated to happen between 15 and 40 years (Agostinho et al. 1999, Agostinho et al. 2016). The richness observed in each SF-IWT reservoirs was at maximum of 29 species, which is close to the average richness of n = 30 found in most Neotropical reservoirs (Agostinho et al. 2007). In general, small diversity and richness are expected for Neotropical impounded areas (Agostinho et al. 2007, Agostinho et al. 2016), especially new ones such as SF-IWT reservoirs. We observed a positive correlation between age and richness. Reservoirs were as richer as they were older. However, despite those observed peaks of richness in the colonization phase of the reservoirs, it is expected that after reaching the stabilization phase, reservoirs older than 20 years present lower richness than the younger ones (Agostinho et al. 2007). Those richness variations are the consequence of several variables such as the reservoir location, distance from the species matrix (rivers), impoundment area, and anthropogenic activities in and around the reservoirs.

Besides age, the reservoirs' location has influenced the fish composition in SF-IWT reservoirs. The main species matrix (São Francisco River), has its water pumped through all SF-IWT canals and reservoirs, serving as a major species pool. However, the East and North Axes reservoirs are surrounded by other basins along their path: the Moxotó, and Pajeú (São Francisco) sub-basins surrounding EA, Ipojuca basin surrounding AB, and the Brígida (São Francisco) sub-basin, Jaguaribe, Apodi-Mossoró, and Piranhas-Açu basins surrounding the NA. The EA had all of its native species originating from the São Francisco River (Silva et al. 2023) since its surrounding basins are mainly subsections of the São Francisco and not independent basins, as seen for the NA. Meanwhile, the four different basins surrounding the NA together with the São Francisco basin, supplied the NA reservoirs with a larger number of species, many exclusive, when compared to the EA. Moreover, the NA catchment is located in a lotic portion of the São Francisco River, which is naturally richer compared to the lentic reservoir catchment of EA. These watershed species matrixes helped determine the distinction in fish assemblage between regions.

The most abundant species were *As. lacustris*, *A. vaillanti*, *C. monoculus*, *H. marginatus, H. brevis, H. gracilis*, *M. costae*, *O. niloticus*, and *P. vivipara*. Following a pattern described in the literature for the Neotropical region, there was a prevalence of specimens from the Characidae family (*As. lacustris*, *M. costae* and *Hemigrammus* spp.), characterized by small-sized sedentary species, with generalist habit, high tolerance, and efficient reproductive strategies (opportunistic *sensu* Winemiller 1989, Agostinho et al. 1999, Agostinho et al. 2007, Dagosta & De Pinna 2019). The second most abundant species was the anchovy *A. vaillanti*. The species demonstrated a great colonization capacity, with fast establishment and spread through all reservoirs. *Anchoviella vaillanti* successful residence in SF-IWT reservoirs can be explained by the species efficient trophic and reproductive strategies (Silva et al. 2023). The other prevalent group, Cichlidae was represented by the non-natives: *O. niloticus* and *Cichla* spp. Cichlids in general present great reproductive, feeding, and abiotic plasticity, as well as high adaptability to lentic environments (Agostinho et al. 2021), being already widely dispersed in many Caatinga-region reservoirs (Costa et al. 2017, Silva et al. 2020, Silva et al. 2023).

Reservoirs assemblages are supposed to be similar to the surrounding basins (Rahel 2007). However, constant man-mediated non-native fish releases in reservoirs cause biotic differentiations (Daga et al. 2015). The ichthyofauna of the SF-IWT reservoirs was composed mainly by species native to the Caatinga domain, except for the non-natives: *O. niloticus*, *P. managuensis*, *C. monoculus*, *C. temensis*, *H. littorale*, *P. reticulata*, *M. lippincottianus*, and *P. squamosissimus.* This is a small but yet very common group of species, constantly released in the Northeast Brazilian reservoirs (for commercial or recreative purposes), that are widely spread in most of the Caatinga domain basins, considered well-established invasive species in the region (Leão et al. 2011, Brito et al. 2020, Silva et al. 2020, D'Avilla et al. 2021). These invasives represented more than 12% of the total abundance in our study, compared to endemics that represented just 9%. As pointed by Agostinho et al. (2007), non-native species are usually more successful in recent reservoirs, such as the SF-IWT reservoirs, mainly due to their resistance and opportunism during environmental disturbances (*e.g.*, reservoir formation), the abundant presence of small preys (*e.g.*, *As. lacustris*, *M. costae,* and *A. vaillanti*), absence of natural predators, and few large competitors present (for Semiarid reservoirs also discussed by Brito et al. 2020). Moreover, the parental care and fractionated-type spawning strategies seen in most of the presented invasives (equilibrium *sensu* Winemiller 1989, Assis et al. 2017, Brito et al. 2020), associated with generalist diet, represent major advantages to establishment in reservoirs (Agostinho et al. 2007). For example, *Oreochromis niloticus* is well known in the literature for dominating reservoirs, being highly prolific, having high resistance to environmental variations (Canonico et al. 2005, Attayde et al. 2011), and contributing to the homogenization of species in invaded sites (Canonico et al. 2005, Leão et al. 2011, Vitule & Prodocimo 2012, Daga et al. 2015). Moreover, the dominance of *Parachromis managuensis* and *Cichla* spp. in some reservoirs may explain the reduced richness and low abundance of native predators (Pelicice & Agostinho 2009), since the invasive predators can inhibit the natives' growth and compete for food resources (Carvalho et al. 2014, França et al. 2017, Resende et al. 2020, Sastraprawira et al. 2020). *Cichla* spp. are also known to succeed in reservoirs due to reproductive strategies, opportunistic feeding behavior, cannibalism of young, and resistance to environmental changes (Gomiero & Braga 2004, Carvalho et al. 2014, D'Avilla et al 2021).

Although crucial on the socioeconomic perspective, the construction of interconnected artificial reservoirs by SF-IWT project raised a major environmental concern: the dispersal of fish species between historically separated basins (Silva et al. 2020). Some recorded species, despite considered native to the Caatinga domain, are exclusively native or endemic to the donor basin, the São Francisco. Therefore, those São Francisco River species were geographically isolated from the receiving basins before the SF-IWT implementation. The spread and introduction of *M. costae* e A. *vaillanti* thought EA reaching the Paraíba do Norte receiving basin was discussed by Ramos et al. (2021) and Silva et al. (2023), however no impact by these species was yet detected. Remarkably, *A. vaillanti* is also spreading through NA and has already been detected in the Jaguaribe basin (in prep.). We also observed the spread of *Cichlasoma sanctifranciscense* through all the EA reservoirs and canals over time, and this species was already registered in the Paraíba do Norte basin in April 2023 (in prep.). Meanwhile, reports of *Megaleporinus obtusidens* in the Paraíba do Norte and Jaguaribe basins are speculated to be accidental, non-related to the SF-IWT, since just one specimen was captured in one reservoir (Tucutu) during all monitoring time, and none along the reservoirs SF-IWT (as seem for *C. sanctifranciscense*). Other São Francisco basin species that did not reach the receiving basins yet but we detected spreading through NA reservoirs are: *Steindachnerina elegans*, *Bryconops* aff. *affinis*, *H. brevis*, and *Roeboides xenodon*. All of those species present efficient life strategies that allow successful spread and colonization in reservoirs (Winemiller 1989, Agostinho et al. 1999, Agostinho et al. 2007). The constant influx of donor-basin-fish-propagules into the SF-IWT reservoirs seems to guarantee a viable propagule number, supporting these opportunistic species to overcome demographic and ecological barriers, determining a successful establishment and spread (Simberloff 2009).

The balance between socioeconomic and environmental benefits/impacts should be extensively discussed prior to implementation of megaprojects such as the SF-IWT. The SF-IWT reservoirs are artificial impoundments especially built to mitigate the shortage of water in the driest region of Brazil and represented a great change in the Caatinga region, bringing water and species to places that were previously dominated by dry lands and intermittent rivers. Those reservoirs constantly undergo several anthropogenic actions, mainly related to water fluctuation and species introduction. The human-induced changes are dramatic in fish colonization and establishment success (Jia et al. 2020). This reinforces the importance of monitoring the reservoirs over time and registering the ichthyofauna development over the years. As the accumulation curves suggested, a continuous effort could reveal additional species, patterns in long-term colonization, and serve as base-data on the reservoirs' future stabilization phase. Our data indicate that the fish fauna from the São Francisco donor basin are the main colonizers of the SF-IWT-created new environments, along with invasive species deliberately released in those sites, and eventual species from the surrounding receiving basins. Considering the presented potential of SF-IWT system to serve as dispersal bridge from donor to receiving basins, prevention measures are key points to minimize introduction risks. To avoid the translocation of species, we reinforce that the physical and electrical barriers described by Silva et al. (2023) should be implemented to mitigate the introduction of new species in the receiving basins. As for species that already reached the previous isolated basins, a continuous and detailed monitoring is essential for management planning and possible impacts assessment.

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Conflicts of Interest

The authors declares that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data availability

The datasets generated during and/or analyzed during the current study are available at: https://doi.org/10.48331/scielodata.ELHXGF and https://sisgen.gov.br/paginas/pubpesqatividade.aspx (Código de Cadastro: A8EC2B0)

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Article

Croton L. (Crotonoideae, Euphorbiaceae) in a protected area in Northeast Brazil

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Abstract: *Croton* is the largest genus of Crotonoideae Burmeist. (ca. 1200 species), with approximately 300 species distributed in all the phytogeographic domains in Brazil. The Chapada of Araripe Environmental Protection Area (CA-EPA) is one of the largest protected areas in northeastern Brazil and comprises many different types of vegetation. Considering the expressive representation of *Croton* in that northeastern region and its morphological complexity, we carried out a taxonomic study of the species occurring in the CA-EPA. The analysis of collections deposited in regional herbaria, together with field observations, revealed 18 *Croton* species, five of which had never been cited as occurring in the study area; seven of those taxa are endemic to the Brazilian semiarid region. *Croton* species were recorded in all of the vegetation types in the CA-EPA, especially in the "carrasco" and "caatinga" vegetation. The plants habits, the shapes of their stipules, extrafloral nectaries, indumenta, and staminate and pistillate sepals were important characteristics for their differentiation.

Keywords: *Caatinga; Chapada do Araripe; Crotonoideae; new records.*

Croton L. (Crotonoideae, Euphorbiaceae) em uma área protegida do Nordeste do Brasil

Resumo: *Croton* é o maior gênero de Crotonoideae Burmeist. (ca. 1200 espécies), com aproximadamente 300 espécies distribuídas em todos os domínios fitogeográficos brasileiros. A Área de Proteção Ambiental da Chapada do Araripe (APA-CA) é uma das maiores áreas protegidas do nordeste brasileiro e compreende diversos tipos de vegetação. Considerando a expressiva representatividade de *Croton* no Nordeste, bem como sua complexidade morfológica, realizamos um estudo taxonômico das espécies ocorrentes na APA-CA. A análise de coleções depositadas em herbários regionais, juntamente com observações de campo, revelou 18 espécies de *Croton*, cinco das quais nunca haviam sido citadas como ocorrendo na área de estudo; sete desses táxons são endêmicos do semiárido brasileiro. As espécies foram registradas em todas as fitofisionomias da APA-CA, principalmente na vegetação de carrasco e caatinga. Os hábitos das plantas, as formas de suas estípulas, nectários extraflorais, indumentos e sépalas estaminadas e pistiladas foram características importantes à diferenciação.

Palavras-chave: *Caatinga; Chapada do Araripe; Crotonoideae; novos registros.*

Introduction

Croton L., the largest genus of Crotonoideae (Euphorbiaceae), comprises almost 1,200 species throughout tropical regions of the world. Its representatives are recognized as sharing clear or colored latex, tectors or glandular trichomes, tectors trichomes can be simple, stellate to lepidote; leaves often with acropetiolar or basilaminar nectaries, Inflorescence thyrsus-like with staminate flowers in the distal portion of the branch and pistillate flowers in the proximal portion, trichomes on the receptacle, curved stamens in the floral buds, and corolla reduced or absent in pistillate flowers (Webster 1993; Berry et al. 2005).

Croton species (popularly known as "marmeleiro" or "velame") are widely used in folk medicine in the semiarid region of northeastern Brazil (Roque et al. 2010) to treat stomach and intestinal disorders, allergies, nasal inflammations, and headaches (e.g., Morais et al. 2006, Ribeiro et al. 2014, Silva et al. 2015), and are known to have antimicrobial, antibiotic, and healing properties (e.g., Lima et al. 2001, Ximenes et al. 2013, Daouda et al. 2014). Medina et al. (2009) demonstrated the efficiency of the essential oil extracted from *C. floribundus* to treat schistosomiasis. Additionally, *C. argyrophyllus* has the potential to combat chikungunya, dengue, zika and other arboviruses transmitted by *Aedes aegypti* (Linnaeus, 1762) (Cruz et al. 2017).

Brazil is one of the centers of endemism of the genus *Croton*, with approximately 300 species distributed in all of its states and phytogeographic domains (Berry et al. 2005; Caruzo et al. 2020). Approximately 110 species are found in northeastern Brazil (ca. 10% of the total diversity of the genus), with most of them occurring in the Caatinga domain (67) (Caruzo et al. 2020). Although *Croton* is one of the most taxonomically studied genera of the Crotonoideae family in Brazil (Secco et al. 2012), especially in the semiarid region (e.g., Carneiro-Torres 2009), there is still much to be discovered, as many new records and new species have recently been published (see Gomes et al. 2010; Carneiro-Torres et al. 2011; Rossine et al. 2020; Sodré & Silva 2022).

The high *Croton* richness and endemism in the Caatinga domain is relentlessly exposed to high levels of anthropic pressure. According to IBGE (2020), that domain showed continuous decreases in both grassland and forested vegetation cover between 2000 and 2018, with more than 35 thousand km² being impacted. Deforestation there has mainly been caused by harvesting firewood and pasture formation (MMA-Atlas 2007). Another worrying situation refers to the low number of legally protected areas in the Caatinga domain, especially in light of its significant territorial extension (Unidades de Conservação 2022).

The Chapada of Araripe Environmental Protection Area (CA-EPA) stands out as a sustainable-use conservation area occupying parts of three states in the Caatinga domain in northeastern Brazil. Despite having been established in 1997, the reserve still does not have a management plan and suffers from deforestation and degradation due to fire and pasture formation, resulting in ecosystem fragmentation (ICMBio 2015; Silva & Souza 2018). An increased knowledge of the occurrence and distribution of its biodiversity would help to identify target taxa for conservation, aid in establishing management strategies, allow the assessment of compliance with its conservation objectives, and help sustain human populations in the region without causing environmental degradation (Ragas 1995; Santos 2018).

Loiola et al. (2015) surveyed the phanerogamic flora of Chapada of Araripe and listed 480 species of Angiosperms belonging to 79 families – especially Fabaceae Lindley (95 spp.), Rubiaceae Jussieu (28 spp.), Euphorbiaceae Jussieu (27 spp.), Bignoniaceae Jussieu (22 spp.), and Asteraceae Berchtold & Jan Presl (19 spp.). *Croton* was the most numerous genus in the entire survey (14 spp.), reflecting its expressive representation in areas of caatinga, cerrado, and humid forest vegetation (Cordeiro et al. 2015; Caruzo et al. 2020) – the vegetation types predominating in the CA-EPA.

The species list first presented for the CA-EPA (Loiola et al. 2015) was not, however, definitive, as some of the municipalities included within the reserve were not included in the survey – making it important to undertake a more detailed and inclusive taxonomic study of the area. Considering then the expressive representation of *Croton* in northeastern Brazil, the morphological complexity of the genus, and the lack of specific studies of that taxon in Chapada of Araripe, we undertook a study of the taxonomic and geographic distribution of *Croton* species occurring in the CA-EPA.

Materials and Methods

1. *Study area*

The Chapada do Araripe Environmental Protection Area (CA-EPA) is a sustainable-use reserve located in the Araripe Basin area in the Caatinga domain; it was established in 1997 under federal jurisdiction within the scope of the National System of Conservation Areas – SNUC) (ICMBIO 2015). The reserve is centered at 7° S and 40°, covers 1,063,000 hectares, overlaps three states (Ceará, Pernambuco, and Piauí), and includes portions of 33 municipalities: Ceará – Abaiara, Araripe, Barbalha, Brejo Santo, Campos Sales, Crato, Jardim, Jati, Missão Velha, Nova Olinda, Penaforte, Porteira, Potengi, Salitre, Santana do Cariri; Pernambuco – Araripina, Bodocó, Cedro, Exu, Granito, Ipubi, Moreilândia, Ouricuri, Santa Cruz, Serrita, Trindade; Piauí – Caldeirão Grande, Curral Novo, Fronteira, Padre Marcos, Paulistana, Pio IX and Simões.

The characteristic climate of the CA-EPA region is hot tropical, with annual temperatures ranging between 23 and 27° C; the period between May and August is somewhat milder, with an average temperature of 21 to 25° C (IPECE 2009). The rainfall regime is irregular (varying from 700 to 1000 mm/year), with heavy concentrations of precipitation within just a few months of the year, with February being the wettest month. Elevations there can reach 850 to 1000 m a.s.l. The CA-EPA includes a number of different vegetation types: caatinga, carrasco, cerradão, cerrado, and humid forest (IBGE 2021).

1.1. Visits to herbaria and data collection

After an online survey of the digital platforms SpeciesLink (http://inct.splink.org.br/) and Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/), seven herbaria were selected for visitation or loan requests. The EAC, HCDAL, HUEFS, IPA, UFP, HST (non-indexed), and PEUFR herbaria (acronyms according to Thiers 2021) contained a considerable number of *Croton* exsiccates from the CA-EPA, and the EAC, HCDAL, HST, and PEUFR herbarium were visited. Exsiccates from the UFP herbarium (UFPE) were analyzed on loan. The other herbaria were not visited for health and safety reasons, due to the SARS-CoV-2 pandemic.

1.2. Species identifications and descriptions

Species identifications and descriptions were made based on consultations with specialists, the specialized literature (Carneiro-Torres 2009; Silva et al. 2010; Sodré et al. 2019; Rossine et al. 2021), and by comparison with standard collections. The descriptions were developed through morphological analyses of the specimens and complemented with information provided on the herbarium labels. If the herbarium specimens from the conservation area were not sufficient to provide detailed descriptions, they were complemented with material collected in the same domain and close to the study region. The terminologies used were based on Hickey (1973), Radford et al. (1974), Harris & Harris (2001), Webster et al. (1996) and Lucena & Sales (2006). Illustrations of the specimens analyzed are provided to demonstrate details of relevant morphological structures. Comments concerning the habitats and geographic distributions of the species were based on information contained on the herbarium labels, from digitized databases, and from the published literature.

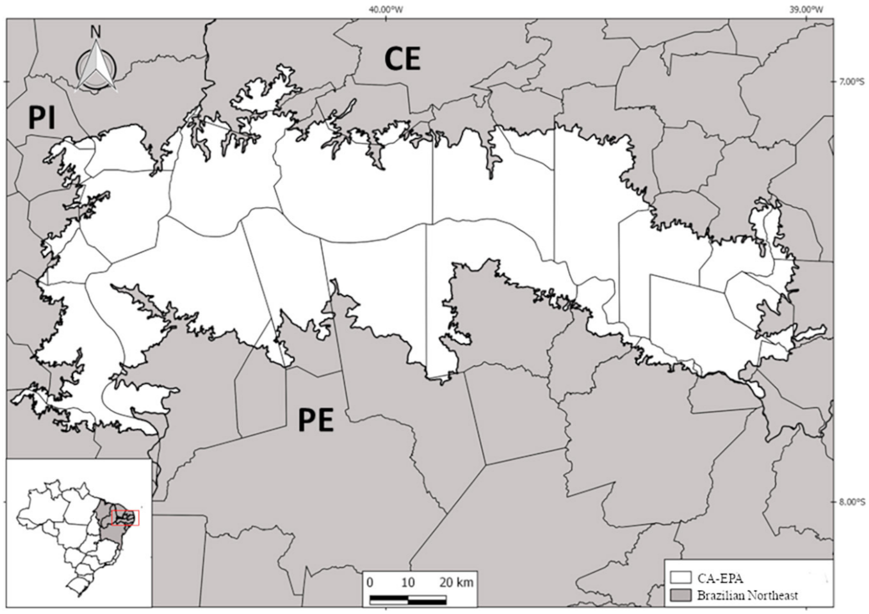

Figure 1. Map showing the location of the Chapada of Araripe Environmental Protection Area (CA-EPA).

1.3. Occurrence data and conservation status

Occurrence data for species were obtained through the analyzed exsiccates and from the SpeciesLink (https://specieslink.net/) and GBIF (https://www.gbif.org/) platforms. The current conservation status of the taxa were verified on the IUCN Red List. When not cited on the endangered species list, conservation data were inferred based on the B criterion of the International Union for Conservation Red List (IUCN 2017), using the GeoCAT platform (http://geocat.kew.org/) (Bachman et al. 2011).

1.4. Maps

The occurrence maps of the species were elaborated using the QGIS program (version 3.8) based on the geographic coordinates obtained for each species, using the shapefiles of Brazil, the northeastern region of that country, and the CA-EPA (available on the website of the Brazilian Institute of Geography and Statistics) (IBGE 2021).

Results

Eighteen species were recorded in the present work: *Croton adamantinus* Müll. Arg., *C. argyrophyllus* Kunth, *C. betaceus* Baill., *C. blanchetianus* Baill., *C. echioides* Baill., *C. floribundus* Spreng., *C. glandulosus* L., *C. grewioides* Baill., *C. heliotropiifolius* Kunth., *C. jacobinensis* Baill., *C. limae* A.P. Gomes, M.F. Sales P.E. Berry, *C. nepetifolius* Baill., *C. pedicellatus* Kunth., *C. sertanejus* Sodré & M.J.Silva, *C. suassunae* Y.Rossine & A.L. Melo, *C. tricolor* Klotzsch ex. Baill., *C. triqueter* Lam. and *C. urticifolius* Lam. Comparing the present survey with that conducted by Loiola et al. (2015), we found five addition new records for the CA-EPA (*C. floribundus*, *C. grewioides, C. sertanejus, C. suassunae*, and *C. urticifolius*). Among the 18 species surveyed in the study area, seven are endemic to the Brazilian semiarid region (*Croton adamantinus*, *C. blanchetianus*, *C. echioides*, *C. jacobinensis*, *C. limae*, *C. sertanejus* and *C. suassunae*).

It was verified that the collection effort in the CA-EPA area is more concentrated among the municipalities of Crato, Barbalha, Jardim, Jati, Brejo Santo, Santana do Cariri, Missão Velha and Nova Olinda, in the state of Ceará; and in the municipalities of Moreilândia, Exu, Araripina, Ipubi, Cedro, Ouricuri and Bodocó, in the state of Pernambuco. All the vegetation types present in the CA-EPA harbor *Croton* species – predominantly in caatinga and carrasco vegetation. *Croton heliotropiifolius* and *C. tricolor* were recorded in all vegetation types present in the CA-EPA, while *C. betaceus* and *C. floribundus* have records only in humid forest environments.

Considering their Extent of Occurrence (EOO), all the species encountered in this study are classified as of Least Concern (LC), based on the B criterion of the IUCN Red List.

In general, the characters most used for species differentiation were, habit, the presence/absence and type of extrafloral nectaries, stipule shape, sepal shape, and staminate petal and pistillate sepal shapes.

Croton L. Sp. Pl. 2: 1004. 1753.
Trees, shrubs, subshrubs or herbs, usually monoecious, with simple, stellate, multiradiate, fasciculate, dendritic and/or lepidote trichomes. Leaves simple, alternate, petiolate, usually with the presence of extrafloral nectaries at the base of the leaf blade or at the apex of the petiole. Presence of stipules. Inflorescence thyrsus-like, terminal, rarely axillary, usually bisexual, with pistillate flowers arranged in the distal portion and staminate in the proximal part of the axis. Staminate flowers pedicellate, dichlamydeous, sepals (5), petals (5), stamens 10 to numerous. Pistillate flowers pedicellate to subsessile, usually monochlamydeous, sepals (5), petals absent or vestigial, styles (3), free or fused at the base, 2-(4)-8 to multifid. Capsule entire or with tripartite columella.

Identification key of *Croton* species occurring in the CA-EPA

1. Extrafloral nectaries absent **2**

1'. Extrafloral nectaries present.. **12**

2. Leaf blade with serrated, sparsely serrated or crenate margins **3**

3. Indumentum with blackish trichomes; leaf blade with serrated to sparsely serrated margins, venation eucamptodromous; stamens 12; sepals of the pistillate flower unequal (3 large and 2 small) and with lacerated margins..17. ***C. triqueter***

3'. Indumentum without blackish trichomes; leaf blade with crenate margins, venation actinodromous; stamens 10; sepals of the pistillate flower equal and with entire margins ....18. ***C. urticifolius***

2'. Leaf blade with margins always entire **4**

4. Herb to subshrub, up to 1 m tall; leaf blade with mucronate apex; inflorescences up to 1.5 cm long ....13. ***C. pedicellatus***

4'. Shrubs to trees, 1–15 m tall; leaf blade with acute, acuminate or rounded apex; inflorescences 1.5–25 cm long.. **5**

5. Abaxial surface of the leaf blade with stellate, stellate-porrect, stellate-dendritic, stellate-lepidote, or fasciculate trichomes **6**

5'. Abaxial surface of leaf blade with lepidote trichomes **9**

6. Stipules lanceolate or oval-lanceolate..**7**

7. Trees, branches with stellate-rotate trichomes, latex absent .... 6. ***C. floribundus***

7'. Subshrubs to shrubs, branches with stellate to stellate-porrect trichomes, latex translucent to orange.........9. ***C. heliotropiifolius***

6'. Stipules auriculate, reniform, or flabellate.. **8**

8. Sepals of the pistillate flower with stellate trichomes on the inner side, ovary with stellate trichomes; seed with rough surface ....10. ***C. jacobinensis***

8'. Sepals of the pistillate flower glabrous on the inner surface, ovary with lepidote trichomes; seed with smooth surface ....4. ***C. blanchetianus***

9. Abaxial surface of the leaf blade yellowish-silvery to silvery, never ferruginous..2. ***C. argyrophyllus***

9'. Abaxial surface of the leaf blade silvery or ferruginous............ **10**

10. Dioecious plants, pistillate sepals spatulate, style bifid ....15. ***C. suassunae***

10' Monoecious plants, pistillate sepals triangular or oblong, style multifid.. **11**

11. Staminate petals elliptic to oblong, pistillate sepals triangular, style 4-fid..11. ***C. limae***

11'. Staminate petals linear-lanceolate, pistillate sepals oblong, style multifid..16. ***C. tricolor***

12. Herbs to subshrubs.. **13**

13. Leaf blade with rounded base, margins crenate to serrate, apex acute, extrafloral nectaries short-stipitate, acropetiolar ....7. ***C. glandulosus***

13'. Leaf blade with cuneate base, margins entire, and apex acuminate to apiculate, extrafloral nectaries sessile, acropetiolar. ....3. ***C. betaceus***

12'. Shrubs **14**

14. Leaf blade with margin entire **15**

15. Acropetiolar extrafloral nectaries 2, eucamptodromous venation, pistillate petals absent .... 5. ***C. echioides***

15'. Acropetiolar extrafloral nectaries 4–6, brochidodromous venation, linear pistillate petals .... 14. ***C. sertanejus***

14'. Leaf blade with margins crenate to double crenate............. **16**

16. Multiradiate trichomes on the abaxial surface of the leaf blade; style 4-6-fid; ovary 4–5 × 4–5 mm.............................. 12. ***C. nepetifolius***

16'. Trichomes stellate to stellate-porrect on the abaxial surface of the limb, style bifid, ovary 2.0–2.5 × 2.0–2.5 mm **17**

17. Bracts 0.7–0.9 mm long, extrafloral nectaries obconical to cylindrical ....8. ***C. grewioides***

17'. Bracts 2.0–3.0 mm long, extrafloral nectaries patelliform .... 1. ***C. adamantinus***

1. *Croton adamantinus* Müller Argoviensis (1873: 115). LECTOTYPE (designated by Sodré et al. 2019):— BRAZIL. Minas Gerais, *campis montanis prope jequitinhonha in distr*., December 1824, *Riedel 1252* (LE00003049!) (Figure 2a, Figure 2c).

Shrub, 1.5–2 m tall, monoecious. Branches pubescent to glabrescent (at maturity), stellate, stellate-porrect, sessile, or stipitate trichomes; latex translucent. Leaves alternate, chartaceous; petiole 0.3–1 cm long, with stellate-porrect trichomes, 2 extrafloral nectaries at apex of petiole, patelliform, short to long-stipitate; stipules 0.5–0.7 cm long, linear, with stellate trichomes; leaf blade 1.2–4.3 × 2.8–8.0 cm, oval, base chordate, margins serrate, apex acute, adaxial surface pubescent to puberulent, abaxial surface woolly to densely pubescent, with stellate trichomes; venation eucamptodromous. Inflorescence 1.4–4.0 cm long, terminal, bisexual; bracts 2.0–3.0 mm long, linear to linear-lanceolate, margins entire, apex acute, glabrous to glabrescent. Staminate flower 2.0 × 2.3–2.8 mm, pedicel 1.6–3.1 mm long, receptacle hirsute, with stellate to stellate-porrect trichomes; sepals 0.9–1.2 × 1.2–2.7 mm, oval, fused at the base, margins entire, apex acute, external surface hirsute-pubescent, with stellate-porrect trichomes, internal surface glabrous; petals 0.8 × 1.5–1.7 mm, oval to lanceolate, glabrescent, margins entire, apex rounded; stamens 10–11. Pistillate flower 2.4–3.0 × 3.5–5.3 mm, pedicel 0.9–4.0 mm long, receptacle hirsute-pubescent, with stellate trichomes; sepals 1.1–2.0 × 2.4–5.3 mm, oval, margins entire, apex acute, external surface pubescent to glabrescent, internal surface hirsute-pubescent to glabrous, with stellate to stellate-porrect trichomes; petals absent. Ovary globose, 2.0–2.5 × 2.0–2.5 mm, hirsute-pubescent, with stellate trichomes; styles bifid. Capsule tomentous, columella with entire apex. Seed globose, ca. 3.0 × 3.0 mm, with surface smooth.

Specimens examined: BRAZIL. CEARÁ: Barbalha, estrada de seu Adão, 7°18'40"S, 39°18'15"W, 26.II.2012, fr., *C. G. Crepaldi, 30* (PEUFR); Barbalha, Estrada de seu Adão, carrasco da floresta nacional do Araripe, 7°18'40"S, 39°18'15"W, 27.I.2012, fr.,

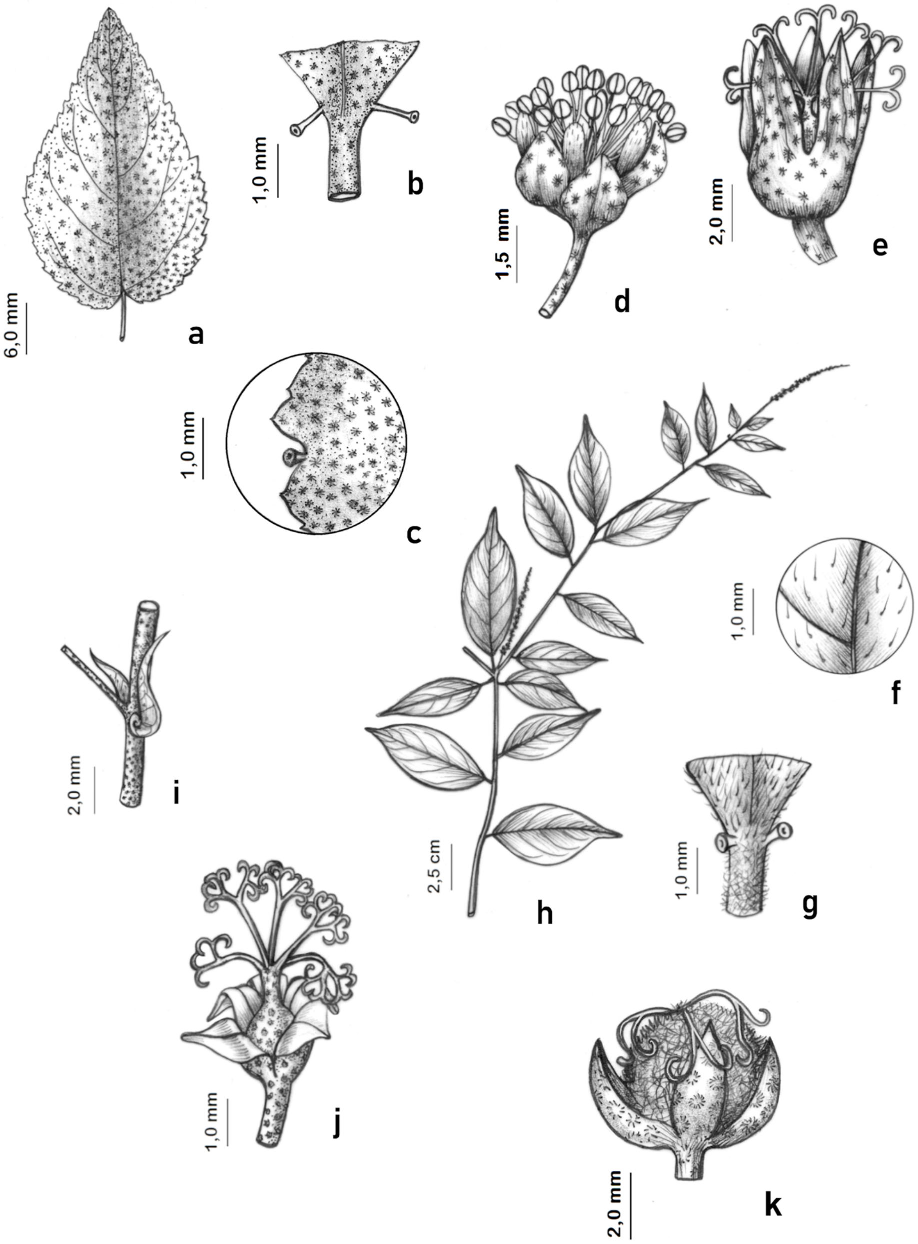

Figure 2. a-c: *Croton adamantinus* Müll. Arg. (Crepaldi C.G. 28) – a. Leaf blade. b-c. Extrafloral nectaries. d-e: *Croton argyrophyllus* Kunth. (K.C. Costa & M.J.N. Rodal 7) – d. Staminate flower. e. Pistillate flower. f-h: *Croton betaceus* Baill. (Walter B.M.T. et al. 6583) – f. Simple trichomes. g. Extrafloral nectaries. h. Habit. i-j: *Croton blanchetianus* Baill. (Araújo P. F. 115) – i. Petiolar stipule. j. Pistillate flower. k: *Croton echioides* Baill. (Oliveira S.F. 11) – k. Pistillate flower. Illustrator: Regina Carvalho.

C. G. Crepaldi, 28 (PEUFR); Barbalha, Estrada de seu Adão, carrasco da floresta nacional do Araripe, 7°18'40"S, 39°18'15W", 02.II.2012, *C. G. Crepaldi, 33* (PEUFR); Barbalha, Malhada Bonita, 7°18'40"S, 39°18'15"W, 02.II.2012 fr., *C. G. Crepaldi, 37* (PEUFR); Crato, 7°14'03"S, 39°24'34"W, 07.V.2019, *L. S. Oliveira, 1* (HST); Crato, Chapada do Araripe, 7°14'03"S, 39°24'34"W, 26.I.2000, fl., *L. W. Lima-Verde, 1907* (PEUFR); Crato, Chapada do Araripe, Saco do Martins, 13.I.1967, fl., *J. S. Sobrinho, 385* (HST); Jardim, Cacimba, 7°34'57"S, 39°17'53"W, 06.VI.2012, *C. G. Crepaldi, 76* (PEUFR); Jati, próximo ao sítio Bacefase, 7°46'08"S, 38°56'58"W, 04.IV.2013, fr., *R. A. Silva, 2752* (HVASF). PERNAMBUCO: Moreilândia, Serra da Mata Nova, Chapada do Araripe, 7°28'13"S, 39°27'58"W, 05.II.2017, *J. F. O. Souza, s.n.* (HCDAL).

Distribution, occurrence in the study area, and conservation status: *Croton adamantinus* is endemic to the Brazilian semiarid region, occurring in the northeastern (in states of Bahia, Ceará, Pernambuco, Piauí, Rio Grande do Norte and Sergipe) and southeastern (Minas Gerais State) areas of that country (Sodré et al. 2019, Caruzo et al. 2020, Riina et al. 2021). It is commonly found in areas of typical caatinga vegetation, as well as in carrasco in the CA-EPA region, at elevations ranging from 555 to 927 m a.s.l. (Figure 3). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 743,049.059 km² and Area of Occupancy (AOO) of 872.000 km².

Notes: *Croton adamantinus* can be distinguished from the other species by having blade with serrate margins and a chordate base, as well as long-stipitate patelliform acropetiolar extrafloral nectaries.

Popular name: marmeleiro-de-rama; marmeleiro-de-carrasco.

2. ***Croton argyrophyllus*** Kunth (1817: 68). TYPE:—VENEZUELA, "crescit in aridis Novae Andalusiae juxta Punta, Araya, Maniquarez et cumana", s.d., *Humboldt s.n.* (Holotype: P P00669843!) (Figure 2d, Figure 2e).

Shrub, 1.0–1.2 m tall, monoecious. Branches glabrous to lepidote, latex absent. Leaves alternate, silver-green, membranous to chartaceous; petiole 0.2–1.8 cm long, lepidote, eglandular; stipules 0.13–0.5 cm long, lanceolate to linear-lanceolate, with lepidote trichomes; leaf blade 0.7–2.0 × 3.7–7.0 cm, elliptic to lanceolate, base slightly chordate, margins entire, apex acuminate, adaxial surface glabrescent, abaxial surface lepidote to glabrescent, indumentum yellowish-silvery to silvery, presence of lepidote trichomes on both faces, venation eucamptodromous. Inflorescence 1.5–10.5 cm long, terminal, bisexual; bracts 1.5–3.0 mm long, linear-lanceolate, margins entire, lepidote. Staminate flower 1.6–2.8 × 1.8–3.2 mm, pedicel 1.2–4.0 mm long, with lepidote receptacle; sepals, ca. 2.0 × 1.7 mm, oval, margins entire, apex acute, external surface lepidote, internal surface glabrous; petals, 2.0–2.3 × 0.5 mm, oblong to lanceolate, margins entire, apex rounded, external surface lepidote, internal surface glabrous; stamens 12–16. Pistillate flower 2.1–4.0 × 3.0–6.0 mm, pedicel 1.2–4.0 mm, receptacle lepidote; sepals 1.1–2.0 × 2.0–5.0 mm, oval, fused at base, margins entire, apex acute, external surface lepidote, internal surface glabrous to glabrescent, with stellate trichomes; petals absent. Ovary globose, 1.8–2 × 1 mm, lepidote; styles multifid, fused at their base, with stellate trichomes at their base. Capsule lepidote, columella with entire apex. Seed ellipsoid, 4.5–4.8 × 3 mm, surface smooth.

Specimens examined: BRAZIL. PERNAMBUCO: Exú, Serra das Abelhas, Chapada do Araripe, 07.V.2013, fl., fr., *M. E. Saraiva, 125* (HST).

Material examinado adicional: BRASIL. CEARÁ: Aiuaba, 6°26'08"S 40°11'32"W, 20.II.2014, *F. K. G. Silva & F. S. Araújo, 12* (EAC). PERNAMBUCO: Venturosa, Parque Pedra Furada, 8°34'30'S 36°52'45"W, 17.I.1998, fl., *K. C. Costa & M. J. N Rodal, 7* (PEUFR). BAHIA: Glória, ca. 4 km de olhos d'Água de Souza, 9°20'37"S 38°18'57"W, 26.IV.2001, fl., *L. P. Queiroz et al., 6529* (HST).

Distribution, occurrence in the study area, and conservation status *Croton argyrophyllus* occurs in Bolivia, Brazil, Colombia, and Venezuela in semiarid environments (Gomes 2006). In Brazil, the species is found in the northeastern region (AL, BA, CE, PB, PE, PI, SE) as well as in some northern states (RO, RR), growing in caatinga and Amazonian savanna vegetation (Caruzo et al. 2020). In the study area, *C. argyrophyllus* was recorded in carrasco and cerradão vegetation (Figure 3). The conservation status of *Croton argyrophyllus* was previously published in the IUCN Red List (2018) as of Least Concern.

Notes: *Croton argyrophyllus* can be confused with *C. limae*, *C. suassunae,* and *C. tricolor*, as they all have branches with a lepidote to glabrous indumentum, absence of glands on the petiole, blades with margins entire, lepidote trichomes on the leaves, stipules, bracts, ovaries, and the receptacles of the staminate and pistillate flowers. They can be distinguished, however, by the shape of the pistillate sepal (oval in *C. argyrophyllus* vs. triangular in *C. limae,* spatulate in *C. suassunae,* and oblong in *C. tricolor*).

3. ***Croton betaceus*** Baillon (1864: 341) LECTOTYPE (designated by Sodré et al. 2017):—BRAZIL. Ceará: sem local, 1838, *G. Gardner 1840* (G 00312269!) (Figure 2f, Figure 2h).

Herbs to subshrubs, 0.4–0.8 m tall, monoecious. Branches glabrescent to hispid, with stellate trichomes; latex translucent. Leaves alternate, membranous; petiole 0.3–1.5 cm long, 2 extrafloral nectaries, patelliform, sessile; stipules 2.0–3.0 mm long, oval-lanceolate, margins entire; leaf blade 1.6–3.9 × 3.5–10.4 cm, elliptic to oblong, base cuneate,

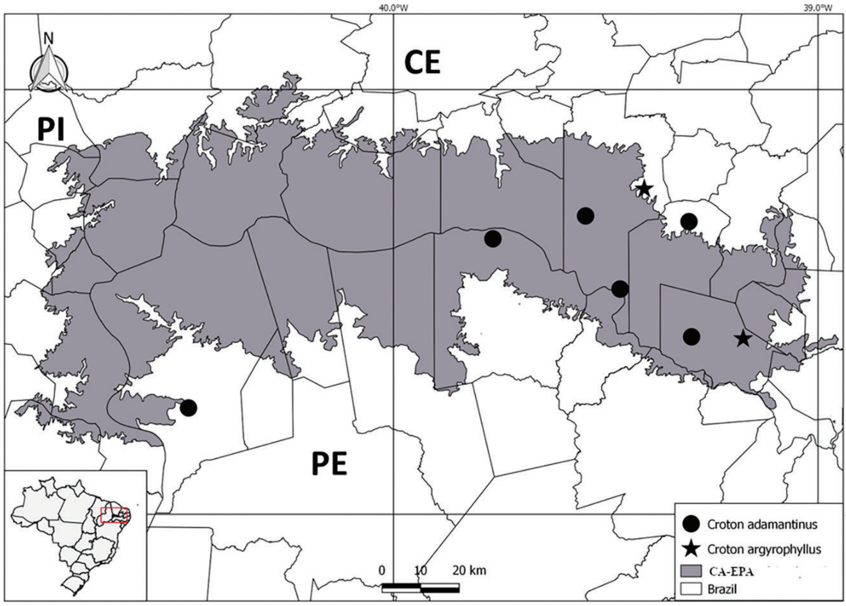

Figure 3. Distribution map of *Croton adamantinus* and *C. argyrophyllus* in the CA-EPA.

margins entire, apex acuminate to apiculate; adaxial face glabrescent to glabrous, with simple trichomes, abaxial face woolly, with stipitate stellate trichomes, venation eucamptodromous. Inflorescence 2.5–11.0 cm long, terminal to axillary, bisexual; bracts 1.0–1.5 mm long, oval-lanceolate, margins entire, apex acuminate, glabrous. Staminate flower 1.5–2.3 × 2.0–3.0 mm, receptacle glabrous to glabrescent, with sparse stellate trichomes; sepals ca. 1.1 × 0.9 mm, oblong to lanceolate, fused at their base, margins entire, apex acute, glabrous to glabrescent, with sparse stellate to stellate trichomes; petals 2.0 × 0.4 mm, elliptic, margins entire, apex acute, glabrous; 11 stamens. Pistillate flower 4.0 × 1.5–2.0 mm, greenish-yellow; sepals 0.6–0.4 × 1.3–2.5 mm, lanceolate to triangular, margins entire, apex acuminate, glabrous, petals absent. Ovary globose, 1.5–2.5 × 1.5–2.5 mm, hirsute, with stellate trichomes, stylets bifid, glabrous. Capsule hirsute, columella with tripartite apex. Seed ellipsoidal, ca. 2–3 × 3–3.6 mm, surface rough.

Specimens examined: BRAZIL. CEARÁ: Barbalha, ladeira de Santana do Cariri, 07.XII.2011, fr., *A. C. B. Santos et al., s.n., s.n.* (HCDAL); Crato, Sítio Guaribas, 18.XI.1998, fl., *E. B. Souza et al. 318* (EAC); Crato, estrada para o granjeiro, Sítio Caiana, Chapada do Araripe, 7°16'30"S 39°26'37"W, 21.I.2014, *B. M. T. Walter et al., 6583* (EAC); Crato, FLONA do Araripe, Guaribas, 14.I.1999, fl., fr., *A. M. Miranda & D. Lima, 3127* (HST).

Additional specimens examined: BRAZIL. CEARÁ: Ubajara, Portal Araticum, Planalto da Ibiapaba – Parna, 24.II.1999, *A. Fernandes et al., s.n.* (EAC); PIAUÍ: Bom Jesus, 17.XII.1977, *A. Fernandes & F. J. A. Matos s.n.* (EAC).

Distribution, occurrence in the study area, and conservation status: *Croton betaceus* occurs in Bolivia, Brazil, and Paraguay. It can be found in the northern, northeastern, midwestern, and southeastern regions of Brazil, growing in the Amazon, Caatinga, and Atlantic Forest (Caruzo et al. 2020). In the northeastern region, it occurs in the states of Bahia, Ceará, Maranhão, and Piauí (Caruzo et al. 2020). In the study area, *C. betaceus* occurs in areas of humid forest vegetation (Figure 4), being frequently recorded along roadsides. The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 3,820,163.055 km² and Endangered when considered its Area of Occupancy (AOO) of 412.000 km².

Notes: *Croton betaceus* can be easily recognized by having a glabrous to glabrescent indumentum on the adaxial face of the leaf blade, and by the presence of simple trichomes on that face, as well as by the leaf blade having a cuneate base and an acuminate to apiculate apex.

Popular name: vassoura-de-urubu.

4. ***Croton blanchetianus*** Baillon (1864: 301). LECTOTYPE: (designated by: Rossine et al. 2021):—BRAZIL. Bahia, without further locality, 1840, *J.S. Blanchet 3094* (P00623615!)) (Figure 2i, Figure 2j). Trees to shrubs, 1–8 m tall, monoecious. Branches hirsute-pubescent to woolly, glabrous at maturity, with stellate-porrect trichomes; latex translucent. Leaves alternate, membranous to papyraceous; petiole 0.5–1.7 cm long, eglandular; stipules 0.2–2.6 cm long, foliaceous, lanceolate to reniform, margins entire; leaf blade 0.2–7.0 × 1.2–13 cm, oval to oval-lanceolate, base chordate to rounded, margins entire, apex acute to acuminate, adaxial surface hispid, pubescent to glabrescent, with stellate-porrect to stellate-lepidote trichomes, abaxial surface hirsute-pubescent to pubescent, with stellate-porrect trichomes, venation eucamptodromous. Inflorescence 2.0–15 cm long, terminal, bisexual; bracts 1.2–3.2 mm long, linear to linear-lanceolate, hirsute, margins entire. Staminate flower 2.5–4.0 × 2.3–3.2 mm, pedicel 2.5–5.0 mm long, greenish yellow, with a lepidote to hirsute-lepidote receptacle; sepals with ca. 2.0 × 1.7 mm, oval, with lepidote or stellate-lepidote trichomes, margins entire, apex acute; petals 2.0–2 × 0.6–0.9 mm, oblong to obovate, margins entire, apex rounded, both faces hirsute to glabrescent; stamens 14–17. Pistillate flower 6.0–7.0 × 4.0 mm, pedicel 1.5–3.0 mm long, greenish-yellow, receptacle lepidote to hirsute-lepidote, with lepidote to stellate-porrect trichomes; sepals 2.5–4.0 × 0.6–1.6 mm, lanceolate, margins entire, apex acute, external surface lepidote to hirsute-lepidote, internal surface glabrous, with stellate trichomes; petals absent. Ovary globose, 2–2.5 × 2–2.5 mm, with

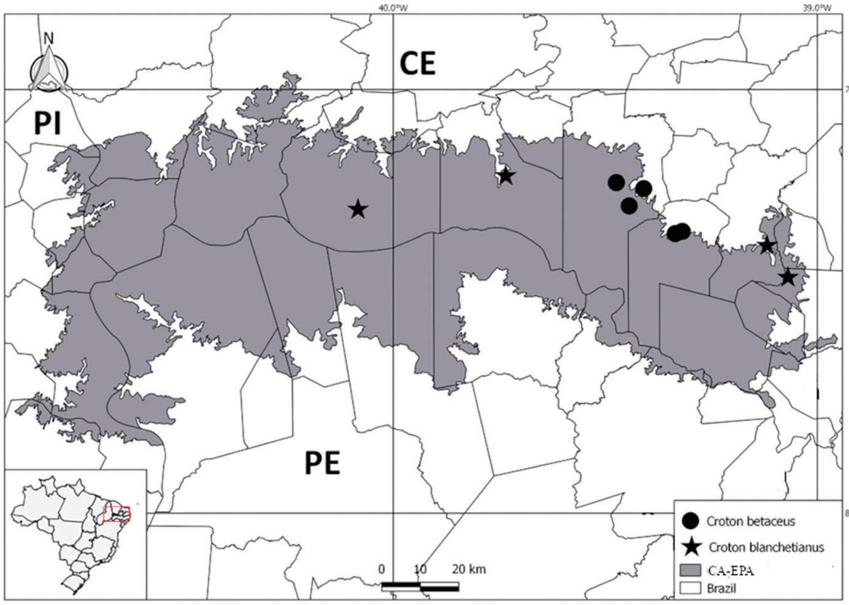

Figure 4. Distribution map of *Croton betaceus* and *C. blanchetianus* in the CA-EPA.

lepidote trichomes; stylets multifid, fused at their base in the form of a column. Capsule lepidote, columella with entire apex. Seed ellipsoidal, 4–6 × 3 mm, surface smooth.

Specimens examined: BRAZIL. CEARÁ: Brejo Santo, Chapada do Araripe, Torres de TV, 7°26'38"S 39°04'08"W, 11.I.2002, fl., *A. P. Fontana, 6285* (HVASF); Jati, Fazenda Oiti, Serra de São Francisco, 7°42'54"S 39°00'23"W, 04.IV.2013, fl., *R. A. Silva, 2725* (HVASF); Santana do Cariri, Subida do Pontal, nos arredores da cidade de Santana, 7°12'15"S 39°44'05"W, 23.I.2014, fl., *B. M. T. Walter et al. 6606, 6607* (EAC). PERNAMBUCO: Araripina, bacia do rio Brígida, topo da chapada, 14.VII.1994, *S. P. Flávia 149* (EAC); Cedro, 7°48'00"S, 39°09'16"W, 28.IV.2019, *Natalia s.n.* (HCDAL). PIAUÍ: Pio IX, cova donga, 6°50'15"S, 40°34'45"W, 21.II.1980, fl., *A. Fernandes s.n.* (EAC).

Distribution, occurrence in the study area, and conservation status: *Croton blanchetianus* is endemic to the Brazilian semiarid region, occurring in the northeastern (in the states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte and Sergipe) and southeastern (Minas Gerais State) regions of that country (Caruzo et al. 2020). It is found in the study area in arboreal caatinga vegetation, at elevations between 394 and 513 m a.s.l. (Figure 4). *Croton blanchetianus* was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 888,791.866 km² and Area of Occupancy (AOO) of 1,856.000 km².

Notes: *Croton blanchetianus* can be identified by having reniform foliaceous stipules, and stylets fused at their base.

Popular name: Marmeleiro-preto.

5. *Croton echioides* Baillon (1864: 334). TYPE:—BRAZIL. Bahia, s.d., *Blanchet 3718* (Holotype: P; isotypes: P, C, K, NY, GDC, BR, A) (Figure 2k).

Shrubs, 1.0–2.0 m tall, monoecious. Branches hirsute to glabrescent, with stellate to stellate-rotate trichomes; latex translucent. Leaves alternate, membranous; petiole 0.5–3.0 cm long, with 2 acropetiolar, patelliform, extrafloral nectaries; stipules 1.2–2.9 mm long, lanceolate, margins entire; leaf blade 1.0–6.6 × 2.0–10 cm, oval to elliptic, base chordate to rounded, margins entire, apex acute to emarginate; adaxial face hirsute to glabrescent, with stellate, stellate-porrect, or simple trichomes, abaxial face tomentose to velutinous, with stellate to stellate-porrect, sessile to stipitate trichomes; venation eucamptodromous. Inflorescence 4.0–27 cm long, terminal, bisexual; bracts 0.9–1.1 mm long, lanceolate, with trichomes, margins entire. Staminate flower 2.0–3.2 × 2.3–2.8 mm, pedicel 3.0–3.2 mm long, receptacle hirsute to glabrescent, with stellate to stellate-porrect trichomes; sepals 1.5–2.0 × 0.8–1.1 mm, elliptic to oblong, margins entire, apex acute, external surface hirsute to glabrous, with stellate trichomes, internal surface glabrous; petals 2.0 × 0.7–0.9 mm, spatulate, glabrous, margins entire, apex rounded; stamens 14–17. Pistillate flower 2.0–2.4 × 1.8–2.5 mm, sessile to subsessile, receptacle hirsute to glabrescent, with stellate trichomes; sepals 1.6–3.0 × 0.8–1.1 mm, elliptic to oval-lanceolate, external and internal surfaces glabrescent, margins entire, apex acute to rounded; petals absent. Ovary globose, 1.5–3.0 × 1.5–3.0 mm, with hirsute-pubescent, stellate trichomes; styles bifid. Capsule globose, pubescent, columella with entire apex. Seed oblong, ca. 5.0 × 2–3 mm, surface rough.

Specimens examined: BRAZIL. CEARÁ: Crato, Flona Araripe, 26.III.1999, *Lima-Verde 1314* (EAC). PERNAMBUCO: Bodocó, 12.II.1991, fl., *P. Lisboa et al. 4515* (EAC); Moreilândia, 7°37'51" S, 39°33'04" W, 11.III.1997, fl., *F. S. Cavalcanti et al. s.n.* (EAC).

Distribution, occurrence in the study area, and conservation status: *Croton echioides* is endemic to the Brazilian semiarid region, occurring in the Caatinga and Cerrado domains, in caatinga vegetation, rupestrian fields, and on rocky outcrops (Caruzo et al. 2020). It is found in the northeastern (in the states of Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí and Rio Grande do Norte) and southeastern (Minas Gerais State) regions of that country (Caruzo et al. 2020). The species can be found in the study area in carrasco and caatinga vegetation (Figure 5). The species was classified as least concern in relation to its extent of occurrence (EOO) of 1,386,692.021 km² and Area of Occupancy (AOO) of 804.000 km².

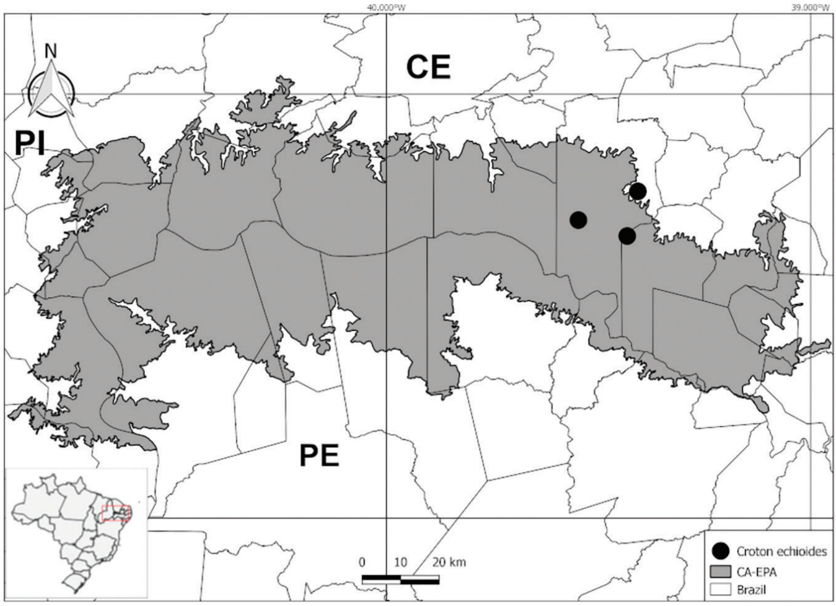

Figure 5. Distribution map of *Croton echioides* in the CA-EPA.

Notes: *Croton echioides* can be recognized by having staminate sepals 1.5–2.0 × 0.8–1.1 mm, elliptic to oblong, and staminate petals spatulate. **Popular name**: velame-preto, canela-de-velho, quebra-faca.

6. *Croton floribundus* Sprengel (1826: 873). NEOTYPE (designated by Caruzo & Cordeiro, 2007):—BRAZIL, São Paulo, *Sellow 171* (SP 18551!) (Figure 6a, Figure 6b).

Tree 2.0–15 m tall, monoecious. Branches hispid, flaky, glabrescent to glabrous, with stellate-rotate trichomes; latex absent. Leaves alternate, membranous to chartaceous; petiole 0.7 × 4.5 cm long, with stellate-rotate trichomes, eglandular; stipules 4.3–5.0 mm long, lanceolate, with stellate-rotate trichomes; leaf blade 0.9–6.5 × 3.5–16.0 cm, elliptic to oval, base oval to attenuated, margins entire, apex acuminate to acute, adaxial face scabridulous to glabrescent, with lepidote trichomes, abaxial face glabrescent, with stellate to stellate-rotate trichomes; venation eucamptodromous. Inflorescence 7.0 × 25 cm long, terminal, bisexual. Bracts 2.0–2.2 mm long, lanceolate. Staminate flower 3.5–4.0 × 3.5 mm, pedicel 4.0–4.3 mm long, receptacle hirsute-pubescent to lepidote, with stellate-rotate to stellate-lepidote trichomes; sepals ca. 3.0 × 1.9 mm, margins entire, apex acute, external surface hirsute-pubescent, with stellate-rotate to stellate-lepidote trichomes, internal surface hirsute, with stellate trichomes; petals ca. 3.0 × 1.1 mm, oblong,

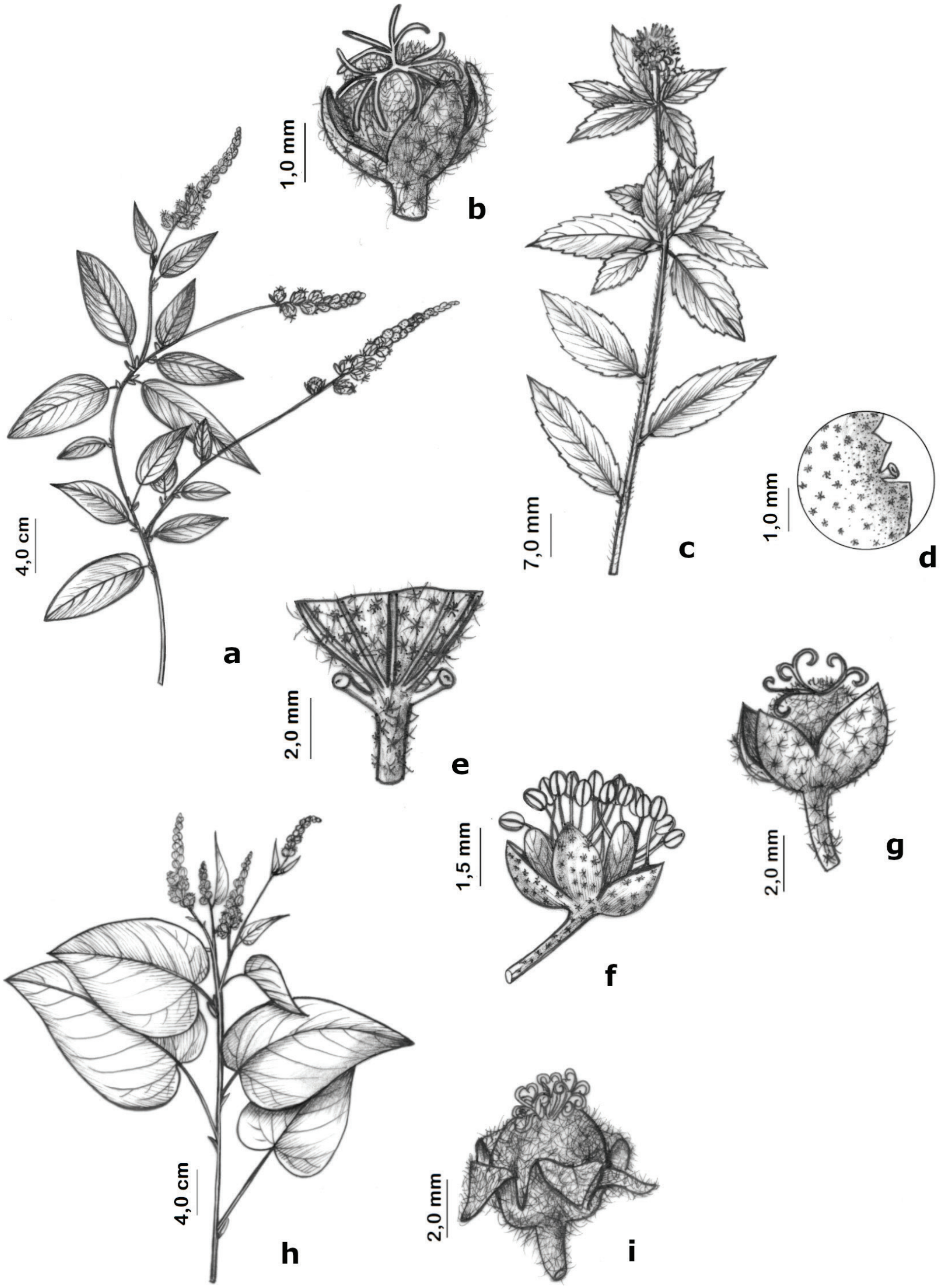

Figure 6. a-b: *Croton floribundus* Spreng. (Rocha E.S. s.n.) – a. Habit. b. Pistillate flower. c-d*:* *Croton glandulosus* L. (Lima-Verde L. W. et al. s.n.) – c. Habit. d. Extrafloral nectaries. e: *Croton grewioides* Baill. (Costa J.G.M. 1619) – e. Extrafloral nectaries. f-g: *Croton heliotropiifolius* Kunth. (Barros, I.O. 6) – f. Staminate flower. g. Pistillate flower. h-i: *Croton jacobinensis* Baill. (T. Plowman 12757) - h. Habit. i. Pistillate flower. Illustrator: Regina Carvalho.

hirsute, with sparse stellate trichomes, margins entire, apex acute; 13 stamens. Pistillate flower 6.5–7.0 × 5.5–6.7 mm, pedicel 0.5–1.0 cm long, receptacle lepidote to hirsute, with stellate-lepidote to stellate-rotate trichomes; sepals ca. 4.0 × 3.8 mm, oval, margins entire, apex acute, external surface lepidote, internal surface glabrous to glabrescent; petals absent. Ovary globose, ca. 3.5–3.5 mm, hirsute, with stellate-rotate trichomes; styles 4-fid. Capsule globose, muricate, columella with entire apex. Seed globose, ca. 5.0–6.5 × 5.0–6.5 mm, surface smooth.

Specimens examined: BRAZIL. Ceará: Crato, Sítio Venha Ver, Chapada do Araripe, Estrada do Belmonte, 7°14'03"S 39°24'34"W, 03.III.2017, *Campos, N. B. s.n.* (HCDAL).

Additional specimens examined: BRAZIL. CEARÁ: Guaramiranga, Subida p/ Mulungu, 13.V.2005, fr., *F. S. Cavalcanti, s.n.* (EAC); Ubajara, Sede Parna, Planalto Ibiapaba, 24.II.1999, *A. Fernandes, et al. s.n.* (EAC); PERNAMBUCO: São Benedito do Sul, Igarapeba, 11.I.1994, fr., *A. M. Miranda, 1152* (PEUFR); São Benedito do Sul, Igarapeba, 11.I.1994, fr., *A. M. Miranda, 1271* (HST).

Distribution, occurrence in the study area, and conservation status: *Croton floribundus* is native to South America, occurring in Brazil and Paraguay in rainforest and riparian forest regions, being commonly found in clearings and along forest edges (Caruzo & Cordeiro 2007; WCSP 2021). The species occurs in northeastern (AL, BA, CE, PB, PE), midwestern (DF, MG, MS), southeastern (ES, MG, RJ, SP), and southern (PA) Brazil, in the Atlantic Forest, riparian vegetation, semideciduous seasonal forests, ombrophilous forests, and anthropized areas (Caruzo et al. 2020). The species was recorded in the study region in humid forest and cerradão (Figure 7). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 2,310,783.550 km² and Area of Occupancy (AOO) of 1,992.000 km².

Notes: *Croton floribundus* can be distinguished from the other species in this study by its arboreal habit, by the presence of stellate-rotate trichomes on the petiole, and by the length of the pedicel of the pistillate flower (5.8–6.0 mm long).

Popular name: Capixingui.

7. *Croton glandulosus* Linnaeus (1759: 1275). LECTOTYPE (designated by Fawcett & Rendle, 1920):—JAMAICA, *Browne*, s.*n.* (Herb. LINN nº 1140.7) (Figure 6c, Figure 6d).

Herbs to subshrubs, 0.2–0.5 m tall, monoecious. Branches hispid to glabrescent, with stellate, stellate-dendritic to stellate-porrect trichomes; latex translucent. Leaves alternate, membranous; petiole 0.2–1.1 cm long, with stellate trichomes, 2 acropetiolar extrafloral nectaries, patelliform, short-stipitate; stipules 1.1–3.0 mm long, linear to oval-lanceolate, margins entire, stellate trichomes may be present; leaf blade 1.1–3.7 × 0.4–2.2 cm, oval to oval-lanceolate, base rounded, margins crenate to serrate, apex acute, adaxial face woolly, with stellate to stellate-dendritic trichomes; abaxial face hirsute tomentose, with stellate-dendritic to stellate-porrect trichomes; venation eucamptodromous. Inflorescence 1.2–4.0 cm long, terminal, bisexual; bracts ca. 1.2 mm long, lanceolate, margins entire, glabrescent, with sparse stellate-porrect trichomes. Staminate flower 1.2–2.1 × 1.2–2.0 mm, pedicel 0.8–2.0 mm long, receptacle hirsute; sepals ca. 0.9 × 0.7 mm, oval, margins entire, apex acute, external surface hirsute to glabrescent, with stellate trichomes, internal surface glabrous; petals ca. 1.1 × 0.6 mm, oval, margins entire, apex rounded, glabrous; stamens 11. Pistillate flower ca. 0.3 × 0.2 cm, pedicel ca. 0.5 mm long, receptacle hirsute, with stellate trichomes; sepals 2.5–4.0 × 0.5–1.0 mm, spatulate, margins entire, apex acute, external surface hirsute to glabrescent, with stellate to stellate-porrect trichomes, internal surface glabrous; petals absent. Ovary globose, 1–1.2 × 1–1.2 mm, with hirsute-pubescent, stellate trichomes, styles bifid, fused at the base. Fruit globose, columella with entire apex. Seed ellipsoidal, ca. 2.5–4 × 2 mm, surface smooth to slightly rough.

Specimens examined: BRAZIL. CEARÁ: Crato, baixa do maracujá, Chapada do Araripe, 7°14'03"S, 39°24'34"W, 02.II.1998, fl., *L. W. Lima-Verde, s.n.* (EAC); Crato, baixa do maracujá, Chapada do Araripe, 02.IV.1998, fl., fr., *L. W. Lima-Verde, et al. 982* (HCDAL). PERNAMBUCO: Moreilândia, sítio Zé de Belina, 10.V.2000, fl., *F. S. Cavalcanti 758* (EAC); Moreilândia, Serra da Mata Nova, Chapada

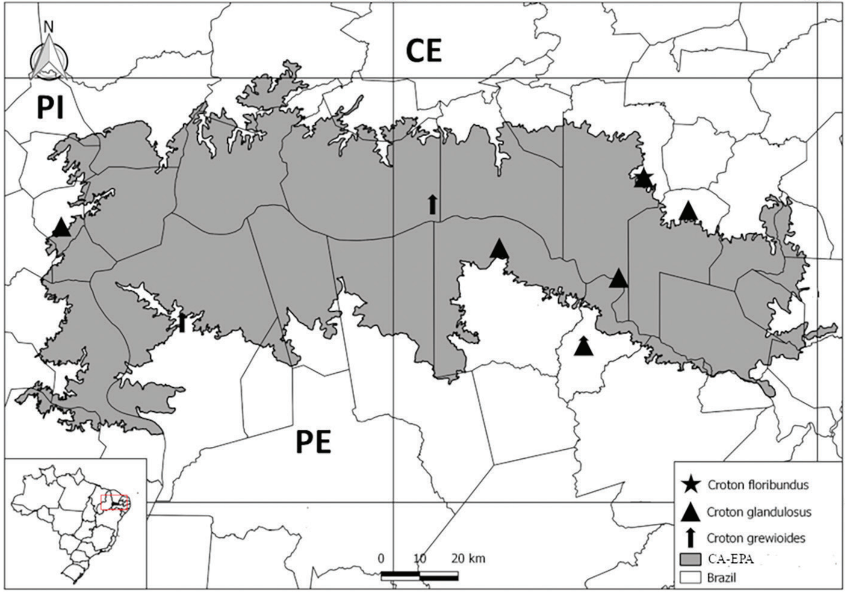

Figure 7. Distribution map of *Croton floribundus*, *C. glandulosus*, and *C. grewioides* in the CA-EPA.

do Araripe, 7°28'14"S 39°28'06"W, 18.III.2017, fr., *J. F. O. Souza, s.n.* (HCDAL).

Distribution, occurrence in the study area, and conservation status: *Croton glandulosus* is native to the Americas and widely distributed, being recorded from the southeastern area of the United States to Argentina (Govaerts et al. 2000, Sodré et al. 2019, Riina et al. 2021, WCSP 2021). *Croton glandulosus* can be found in all regions and in all the Brazilian states, including the Federal District, and in all its phytogeographic domains (Sodré et al. 2019, Caruzo et al. 2020). The species was recorded in the study area in areas of caatinga vegetation and in cerradão, generally in open environments and along roadsides (Figure 7). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 29,382,942.480 km² and Area of Occupancy (AOO) of 2,884.000 km².

Notes: *Croton glandulosus* can be recognized as herbs or subshrubs 20 to 50 cm tall, by the presence of two acropetiolar, short-stipitate patelliform extrafloral nectaries, and by the spatulate sepals of the pistillate flower.

Popular name: gervão-branco, carvão-branco.

8. ***Croton grewioides*** Baillon (1864: 365). LECTOTYPE (designated by Sodré et al. 2019):—BRAZIL. Bahia, 1840, *J. S. Blanchet 3100* (P00623585!) (Figure 6e).

Shrubs, 0.8–2.0 m tall, monoecious. Branches glabrous to glabrescent, with translucent latex. Leaves alternate, membranous; petiole 2.0–8.0 mm long, with stellate to stellate-porrect trichomes, 2 extrafloral nectaries, patelliform; stipules 1.2–3.0 mm long, elliptic, deciduous at maturity; leaf blade 0.8–2.4 × 0.8–6.0 cm, oval, rarely rounded, base rounded, margins crenate, with obconic to cylindrical glands on the margins, apex acute, rarely rounded, adaxial face slightly hispid to sparse-pubescent, with stellate-porrect and stellate-dendritic trichomes, abaxial face tomentose, with stellate-porrect trichomes; venation eucamptodromous. Inflorescence 1.0 × 5.5 cm long, terminal, bisexual; bracts 0.7–0.9 mm long, entire, linear to lanceolate, with stellate to stellate-porrect trichomes. Staminate flower 2.4–2.7 × 2.2–2.8 mm, pedicel 1.3–2.0 mm long, receptacle hirsute, with stellate-porrect trichomes; sepals 0.6–1.1 × 1.2–1.4 mm, oval, outer surface hirsute, with stellate-porrect to stellate-dendritic trichomes, inner surface glabrous to glabrescent, with sparse stellate-porrect trichomes; petals 0.6–0.8 × 1.2–1.3 mm, oblong, glabrous, margins entire, apex rounded; stamens 10–11. Pistillate flower ca. 2.0 × 2.4 cm, pedicel 1.5–2.1 mm long; sepals 0.7–1.1 × 1.9–2.1 mm, lanceolate to oval-lanceolate, hirsute, with stellate to stellate-porrect trichomes, margins entire, apex acute; petals absent. Ovary globose, 2–2.3 × 2–2.3 mm, hirsute, with stellate to stellate-porrect trichomes; styles bifid. Capsule globose, puberulent, columella with entire apex. Seed globose, 2.5–3 × 2.4–2.8 mm, surface smooth.

Specimens examined: BRAZIL. CEARÁ: Crato, sítio Venha Ver, Chapada do Araripe, 7°14'03"S 39°24'34"W, 09.III.1995, *M. A. P. Silva, et al. s.n.* (HCDAL). PERNAMBUCO: Exu, topo da rampa, início do planalto, Chapada do Araripe, 01.02.1984, *G. Fotius & S. Iêdo, 3727* (IPA).

Additional specimens examined: BRAZIL. PERNAMBUCO: Belo Jardim, Estrada do Araçá, 26.V.1993, *A. M. Miranda, et al. 747* (PEUFR); Buíque, Fazenda Brejo de São José, próximo às inscrições rupestres, VII.2005, fl., fr., *A. M. Laurênio & A. P. S. Gomes, 2018* (PEUFR); Ibimirim, estrada Ibimirim-petrolândia, 11.XII.1995, fl., *A. M. Laurênio et al. 288* (PEUFR); Ibimirim, Serra Negra, proximidades do Sítio Oliveira, 22.III.1994, fl., fr., *S. I. Silva, 351* (PEUFR). PIAUÍ: Canto do Buriti, Pajeú, 09.XII.1979, fl., *M. R. Dellaco, s.n.* (PEUFR); Pedro IV, depois de Sertão de dentro, 01.III.1980, *A. J. Castro et al. s.n.* (PEUFR).

Distribution, occurrence in the study area, and conservation status: *Croton grewioides* is native to South America, occurring in Brazil, Bolívia and Peru. (Silva et al. 2010, Sodré et al. 2019, Riina et al. 2021); it occurs widely in all the states of the northeastern region of Brazil and can also be found in Minas Gerais State in southeastern Brazil (Sodré et al. 2019, Caruzo et al. 2020, Riina et al. 2021). The species was recorded in areas of caatinga and carrasco vegetation in the region and is frequently found along roadsides (Figure 7). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 5,489,855.241 km² and Area of Occupancy (AOO) of 924.000 km².

Notes: *Croton grewioides* can be identified by the presence of obconic to cylindrical extrafloral nectaries on the margins of the leaf blade, and by the absence of stipules on mature branches. The species has a characteristic cinnamon scent, as noted by collectors on most herbarium specimen labels.

Popular name: canelinha-de-cheiro, canelinha.

9. ***Croton heliotropiifolius*** Kunth (1817: 83). TYPE: —PERU. "in Calidis apricis Prov. Bracamorensis prope pagum Chamaya et in ripa fluminis 114 Chinchipe, alt. 210 hex", s.d., *A. von Humboldt & A. Bonpland, s.n.* (Holotype: P P00669881) (Figure 6f, Figure 6g).

Subshrubs to shrubs, 1.0–2.0 m tall, monoecious. Branches hirsute-hispid to hirsute-pubescent, with stellate to stellate-porrect trichomes; latex translucent to orange. Leaves alternate, membranous, papyraceous or chartaceous; petiole 0.2–3.0 cm long, eglandular; stipules 1.8–3.0 mm long, oval-lanceolate, margins entire; leaf blade 0.9–6.3 × 1.9–11 cm, oval, oval-lanceolate to obovate, base ovate to rounded, margins entire, apex acute to acuminate, adaxial surface hispid, sparse-pubescent to pubescent, abaxial face hispid to velutine, with stellate, sessile, or stipitate trichomes; venation eucamptodromous. Inflorescence 1.5–17 cm long, terminal, bisexual; bracts 0.8–2.3 mm long, lanceolate, with stellate trichomes; margins entire. Staminate flower ca. 3.0 × 2.0 mm, pedicel 2.0–3.2 mm long, receptacle hirsute to glabrescent; sepals ca. 1.8 × 1.0 mm, ovate, margins entire, apex acute, external surface bristly to glabrescent, with sparse stellate trichomes, internal surface glabrous; petals 2.0–2.2 × 0.8–0.9 mm, oblong, margins entire, apex rounded, glabrous; stamens 15–17. Pistillate flower 2.5–6.0 × 1.5–2.5 mm, pedicel 0.5–1.5 mm long, receptacle hirsute to hirsute-pubescent, with stellate trichomes; sepals ca. 2.0 × 0.8 mm, lanceolate, margins entire, apex acute, external face hirsute, with stellate trichomes, internal face glabrous; petals absent. Ovary globose, 1–2 × 1–2 mm, hirsute-pubescent, with stellate to stellate-porrect trichomes; styles bifid. Capsule villous with columella with tripartite apex. Seed ellipsoidal, 4.0–4.5 × 2.0 mm, surface smooth.

Selected specimens: BRAZIL. CEARÁ: Crato, estrada do belmonte, sítio Venha Ver, Chapada do Araripe, 7°14'03"S, 39°24'34"W, 22.II.2017, fr., *N. B. Campos, 29* (HCDAL); Chapada do Araripe, 7°14'03"S, 39°24'34"W, 25.I.2000, *L. W. Lima-Verde, 616* (PEUFR); Jardim, 7° 29' 36"S 39°22'02"W, 31.VIII.2012, *R. S. Sousa, & L. G. S. Nascimento, 195* (PEUFR); Santana do Cariri, Geoparque Pedra do

Cariri, 7°07'18"S 39°41'42"W, 23.I.2014, fl., *C. E. B. Proença et al. 4708* (UB). PERNAMBUCO: Exú, Serra do Araripe, além do Exú velho, 06.V.1971, fl., *E. P. Heringer et al., 603* (PEUFR); Moreilândia, Serra da Mata Nova, Chapada do Araripe, 7°28'17"S, 39°28'14"W, 03.IV.2016, *J. F. O Souza, s.n.* (HCDAL).

Distribution, occurrence in the study area, and conservation status: *Croton heliotropiifolius* is native to Brazil, occurring in other countries in South America, Central America, and Mexico (WCSP 2021). It occurs in all of the states of northeastern Brazil and has also been recorded in the midwestern (DF, GO) and southeastern (MG) regions of that country (Caruzo et al. 2020). In the study area, *C. heliotropiifolius* can be found in the vegetation types of caatinga, carrasco, cerradão, and cerrado, at elevations ranging from 511 to 1327 m a.s.l. (Figure 8). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 2,154,331.304 km² and Area of Occupancy (AOO) of 1,968.000 km².

Popular name: velame.

10. *Croton jacobinensis* Baillon (1864: 302). LECTOTYPE (designated by Rossine et al. 2021):— BRAZIL. Bahia, Jacobina, 1845, *J.S. Blanchet 3661* (P (P00623531!) (Figure 6h, Figure 6i).

Shrubs to subshrubs, 0.9–2.0 m tall, monoecious. Branches pubescent, sparse-pubescent to glabrescent, with stellate trichomes; latex translucent. Leaves alternate, membranous; petiole 0.3–9.5 cm long, pubescent, woolly to glabrescent, with stellate trichomes, eglandular; stipule ca. 1.0 cm long, foliaceous, lanceolate, auriform to flabelliform, margins entire; leaf blade 1.5–10.6 × 2.9–24.5 cm, cordate, base chordate, margins entire, apex acuminate, adaxial surface puberulent, slightly hispid or glabrescent, with fasciculated stellate trichomes, abaxial surface sparse-pubescent, with stellate to fasciculate, sessile or stipitate trichomes, venation actinodromous. Inflorescence 2–15 cm long, terminal, bisexual; bracts 2–3 mm long, oval-lanceolate, margins entire, apex acute. Staminate flower 4.5–5.0 × 3.5–4.0 mm, pedicel 5.0–7.0 mm long, receptacle pubescent, with stellate trichomes; sepals ca. 3.2 × 1.3 mm, entire, oval, external surface pubescent, internal surface hirsute-pubescent, with stellate, stellate-lepidote to stellate-stipitate trichomes on both surfaces; petals ca. 2.2 × 1.2 mm, oval, external and internal surfaces pubescent, with stellate trichomes; stamens 15–16. Pistillate flower 4.8–7.0 × 4.2–4.8 mm, pedicel 0.7–1.5 mm long, receptacle densely pubescent, with stellate trichomes; sepals ca. 4.2–6.0 × 2.2 mm, entire, oval, margins entire, apex acute, outer surface densely pubescent, inner surface hirsute-pubescent to densely pubescent, with stellate to stellate fasciculate trichomes on both sides; petals absent. Ovary globose, 2.5–3 × 2.5–3 mm, hirsute pubescent to densely pubescent, with stellate trichomes, sessile to stipitate; styles multifid. Capsule pubescent, columella with entire apex. Seed globose, 4.0–8.0 × 4.0–8.0 mm, surface rough.

Specimens examined: BRAZIL. CEARÁ: Barbalha, trilha do pensador, Cariri, 04.II.2011, fl., *M. S. Macedo, s.n.* (HCDAL); Barbalha, 03.03.2018, fl., *A. K. L. S. Pereira, s.n.* (HCDAL); Crato, 11.III.1997, fl., *E. Silveira, s.n.* (EAC); Crato, arredores da Escola Agrícola Federal, 26.V.1993, *M. Andrade-Neto, 32* (EAC); Crato, arredores do Crato, 09.III.1987, *A. Fernandes & Edilberto, s.n.* (EAC); Crato, Chapada do Araripe, 7°14'03"S, 39°24'34"W, 21.XII.1978, *A. Fernandes et al., s.n.* (EAC); Crato, clube recreativo granjeiro, saída do clube, margem direita da estrada, 30.VIII.1998, fl., *M. I. B. Loiola et al., 489* (PEUFR); Crato, estrada para o granjeiro (clube). Sítio Caiana, arredores da cidade de Crato, Chapada do Araripe, 7°16'30"S 39°26'37"W, 21.I.2014, fr., *B. M. T. Walter et al., 6579* (EAC); Jardim, cerrado da FLONA do Araripe, 7°34'57"S, 39°17'53"W, 03.XI.2012, *C. G. Crepaldi, 35* (PEUFR); Crato, Parque Nacional do Araripe, 7°14'03"S, 39°24'34"W, 19.I.1983, fl., *T. Powman, 12757* (EAC); Crato, FLONA do Araripe, Guaribas, 14.I.1999, fl., fr., *A. M. Miranda*, *3140* (HST). PERNAMBUCO: Exu, bacia do Rio Brígida, encosta da Chapada, 16.07.1994, *F. S. Pinto, 214, 224* (EAC); Moreilândia, serra da Mata Nova, 7°30'58" S, 39°29'12"W, 12.II.2016, *J. F. O. Souza, s.n.* (HCDAL).

Distribution, occurrence in the study area, and conservation status: *Croton jacobinensis* is endemic to Brazil, restricted to the semiarid

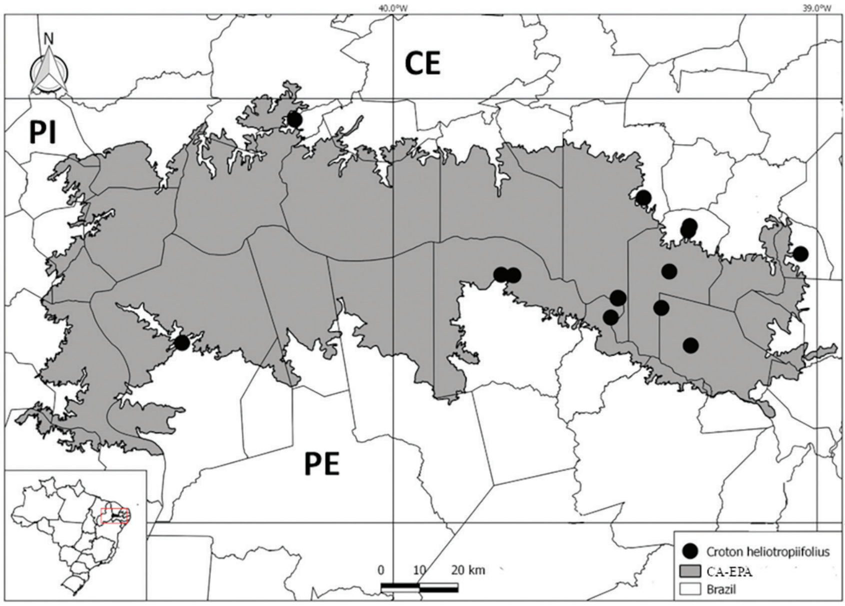

Figure 8. Distribution map of *Croton heliotropiifolius* in the CA-EPA.

region, occurring in the states of Bahia, Ceará, Paraíba, Pernambuco, Piauí and Rio Grande do Norte (Caruzo et al. 2020). The species has also been recorded in Minas Gerais state in southeastern Brazil (Caruzo et al. 2020). The species was recorded in the study area in regions of altered humid forest vegetation and is commonly found along forest edges and riverbanks (Figure 9). It was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 933,844.969 km² and Endangered when considered its Area of Occupancy (AOO) of 488.000 km².

Notes: *Croton jacobinensis* can be identified by having cordate leaves, auriform or flabelliform foliaceous stipules, and a densely pubescent receptacle in the pistillate flower.

Popular name: velame-preto, marmeleiro-preto.

11. *Croton limae* A. P. Gomes, M. F. Sales & P. E. Berry (2010: 206). TYPE:—BRAZIL. Bahia, Município Andaraí, Pai Inácio, 18 fevereiro 1997, *M. L. Guedes 5857* (Holotype: HUEFS!; isotypes: CEPEC, IBGE, MO, NY, PEUFR, USP) (Figure 10a, Figure 10b).

Trees to shrubs, 1.0–10.0 m tall, monoecious. Branches lepidote to glabrous, with lepidote trichomes. Leaves alternate, membranous; petiole 0.2–2.3 cm long, with lepidote to stellate-lepidote trichomes, eglandular; stipules 0.4–2.5 mm long, oval to oval-lanceolate, margins entire; leaf blade 0.8–3.3 × 2.0–7.5 cm, base slightly chordate, oval, margins entire, apex acute, adaxial and abaxial faces lepidote, silvery; venation eucamptodromous. Inflorescence terminal, monoecious; bracts 1.0–1.1 mm long, oval to oval-lanceolate, lepidote, with lepidote trichomes, margins entire. Staminate flower ca. 2.3 × 2.5 cm, subsessile, receptacle lepidote; sepals ca. 0.8 × 1.0–1.1 mm, oval, fused at base, external surface lepidote, internal surface glabrous; petals 4–4.2 × 0.8–1.0 mm, elliptic to oblong, with lepidote trichomes on the outer surface. Pistillate flower ca. 3.0 × 2.8 mm, subsessile, receptacle lepidote; sepals ca. 1.2 × 1.7–2.0 mm, triangular, fused at base, margins entire, apex acute, external surface lepidote, internal surface glabrous; petals absent. Ovary globose, 2.0–2.8 × 2.0–2.8 mm, lepidote; styles 4-fid, united at their base. Capsule globose, columella with entire apex. Seed globose, 4.0–5.0 × 4.0–5.0 mm, surface smooth.

Specimens examined: BRAZIL. CEARÁ: Crato, área de cerrado da Chapada do Araripe, 7°14'03"S, 39°24'34"W, 09.IV.2013, *B. V. Almeida, s.n.* (HCDAL). PERNAMBUCO: Moreilândia, Serra da Mata Nova, Chapada do Araripe, 7°28'10"S, 39°28'02"W 29.V.2016, *J. F. O. Souza, s.n.* (HCDAL). PIAUÍ: Padre Marcos, Serra Velha, 08.IV.1993, fl., *M. E. Alencar, s.n.* (EAC). PERNAMBUCO: Ipubi, Serrolândia, 20.IV.2017, fr., *J. E. L. Torres & W. B. Santos, 76* (HST).

Distribution, occurrence in the study area, and conservation status: *Croton limae* is endemic to the Brazilian semiarid region, occurring in the northeastern area of that country in the states of Bahia, Ceará, Paraíba, Pernambuco, Piauí and Sergipe, in typical caatinga vegetation and carrasco (Caruzo et al. 2020). The species occurs in the study area in caatinga and carrasco vegetation at elevations between 420 and 967 m a.s.l. (Figure 9). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 327,115.107 km² and Endangered when considered its Area of Occupancy (AOO) of 228.000 km².

Notes: *Croton limae* can be confused with *C. argyrophyllus*, *C. suassunae,* and *C. tricolor,* as discussed in the observations concerning the species *C. argyrophyllus*.

Popular name: marmeleiro-branco, marmeleiro.

12. *Croton nepetifolius* Baill., Adansonia 4: 344.1864. LECTOTYPE (designated by Sodré et al. 2019):—BRAZIL. Minas Gerais: s.d., *Saint-Hillaire cat. B2 2115* (P 00634517!) (Figure 10c, Figure 10e).

Herbs to shrubs, 0.6–2.0 m tall, monoecious. Branches hirsute to glabrescent, glabrous when mature, with stellate-porrect trichomes; latex translucent. Leaves alternate, membranous to chartaceous; petiole 0.3–1.8 cm long, with obconic and subsessile extrafloral nectaries at the apex; stipules 0.3–0.9 cm long, linear-lanceolate; leaf blade 0.5–6.1 × 1.0–10.3 cm, oval, base slightly chordate, margins double crenate, presence of obconic extrafloral nectaries, apex acute to acuminate,

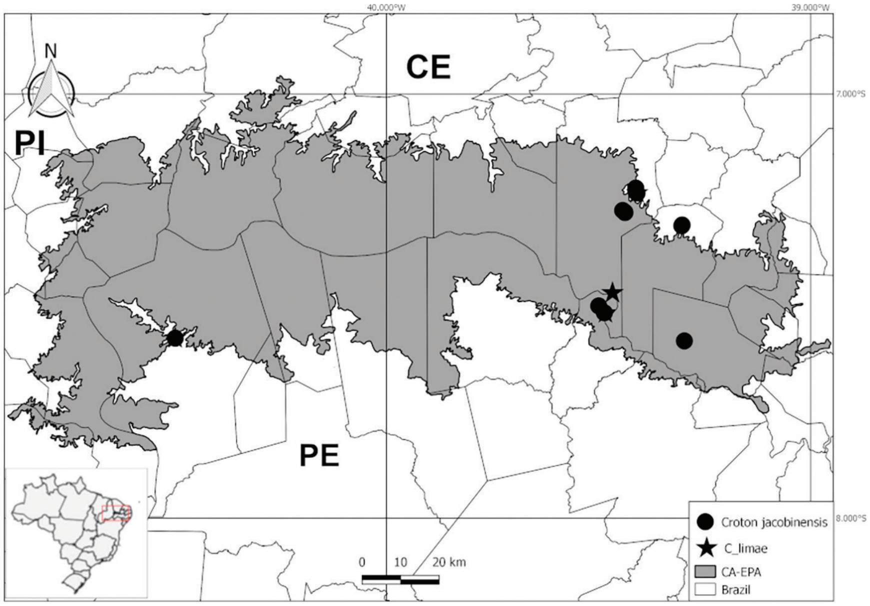

Figure 9. Distribution map of *Croton jacobinensis* and *C. limae* in the CA-EPA.

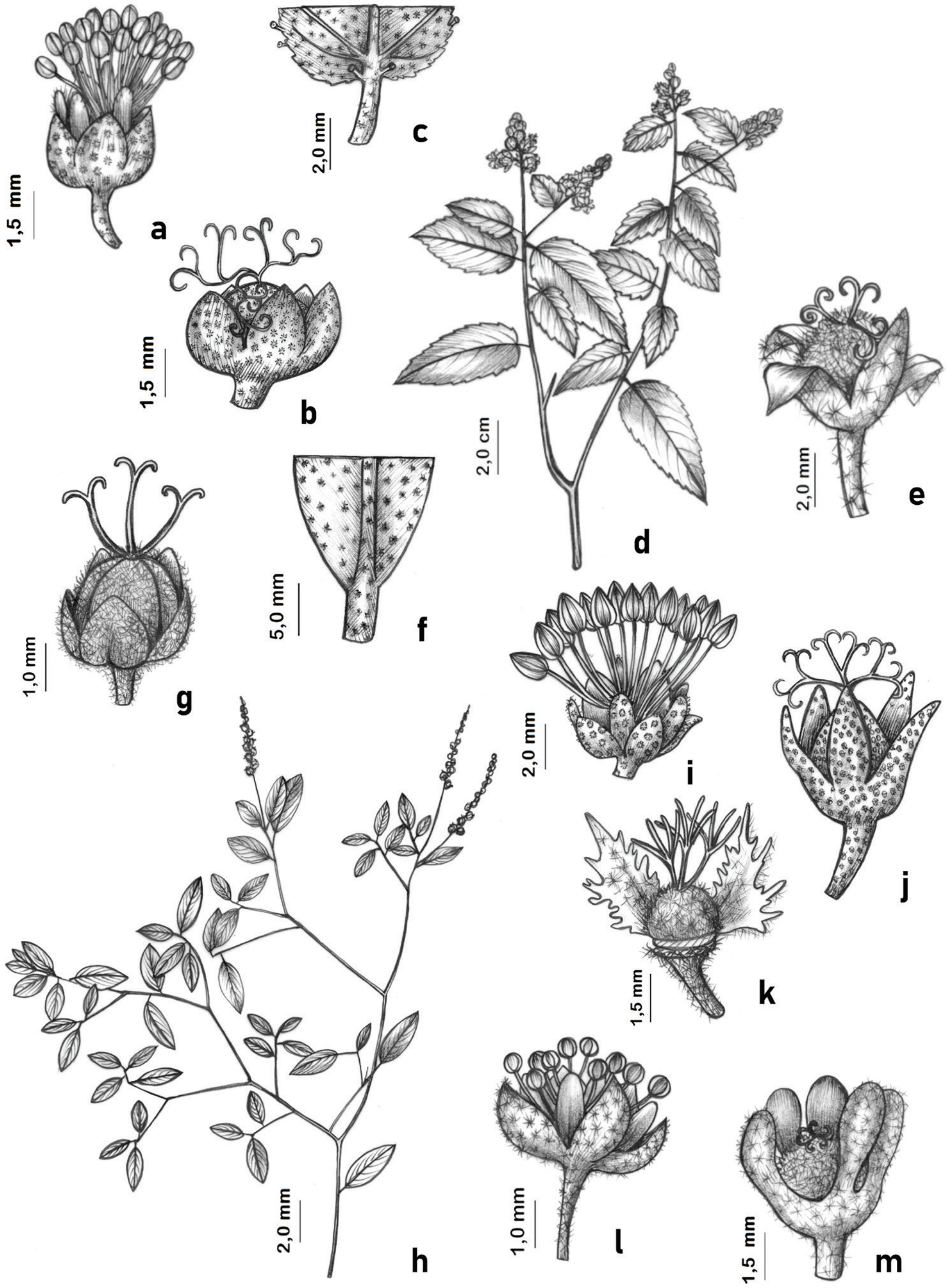

Figure 10. a-b: *Croton limae* A.P.Gomes, M.F.Sales & P.E.Berry. (J. E. L. Torres & W. B. Santos, 76) – a. Staminate flower. b. Pistillate flower. c-e: *Croton nepetifolius* Baill. (Morais Mendonça et al. s.n.) – c. Extrafloral nectaries. d. Habit. e. pistillate flower. f-g*: Croton pedicellatus* Baill. (Cavalcanti F. S. & Andrade M 33 (106) – f. Trichomes at the base of the leaf blade. g. Pistillate flower. h: *Croton suassunae* Y. Rossine & AL Melo. (T.R. Leite 9131) 9 1 - h. Habit. i-j: *Croton tricolor*. Klotzsch. ex bail. (A. Fernandes & F. J. Matos) – i. Staminate 2 flower. j. Pistillate flower. k: *Croton triqueter* Lam. (Cavalcanti F.S. s.n.) – k. Pistillate flower. 3 l-m: *Croton urticifolius* Lam. (A.M. Miranda 1192) – l. Staminate flower. m. Pistillate flower. Illustrator: Regina Carvalho.

adaxial face hirsute-hispid to hirsute-pubescent, with stellate-porrect trichomes, abaxial face hirsute-pubescent, with multiradiate stellate trichomes, venation actinodromous. Inflorescence 0.8–5.0 cm long, terminal, bisexual; bracts ca. 3 mm long, linear-lanceolate, with stellate trichomes. Staminate flower 1.7–3.0 mm long, pedicel 0.8–1.0 mm long, cream-colored, hirsute to glabrescent; sepals 1.2–1.7 mm long, oval, margins entire, apex acute, hirsute to glabrescent, with stellate trichomes on outer surface and apical portion of inner surface; petals 0.9–1.8 mm long, oblong, margins entire, apex acute to rounded, glabrous; stamens 10–12. Pistillate flower 3.8–5 mm long, pedicel 3.2–4.0 mm long, receptacle pubescent; sepals 1.1–2.9 mm long, oblong, margins entire, apex acute, hirsute-pubescent to glabrescent on the outside and glabrescent on the inside, with stellate trichomes on both faces; petals absent. Ovary globose, 4–5 × 4–5 mm, hirsute-pubescent, with stellate trichomes; styles 4–6-fid. Capsule tomentous with columella with entire apex. Seed globose, 4.0–5.5 × 4.0–5.5 mm, surface smooth.

Selected specimens: BRAZIL. CEARÁ: Barbalha, trilha da cruz vermelha, 7°27'32"S, 39°20'18"W, 11.VII.2007, fl., *M. A. P. Silva,* *et al. s.n.* (HCDAL); malha bonita, Cariri, 07.XII.2011, *A. B. C. Santos, s.n.* (HCDAL); Crato, Chapada do Araripe, 7°14'03"S, 39°24'34"W, 26.III.1999, *L. W. Lima-Verde, 1322* (PEUFR), São Mindimba, Chapada do Araripe, 07.III.2007, fl., *E. R. Silveira & F. S. Cavalcanti, 1061* (EAC); Jardim, carrasco da FLONA, 7°34'57'S, 39°17'53"W, 09.II.2012, *C. G. Crepaldi, 45* (PEUFR). PERNAMBUCO: Moreilândia, Serra da Mata Nova, Chapada do Araripe, 7°28'11"S 39°28'00"W, 06.II.2016, *J. F. O. Souza, s.n.* (HCDAL).

Distribution, occurrence in the study area, and conservation status: *Croton nepetifolius* is native to Brazil, also occurring in Bolivia and Venezuela (Sodré et al. 2019, Riina et al. 2021, WCSP 2021). The species can be found in all northeastern Brazilian states and in Minas Gerais in the southeast, in the Caatinga and Atlantic Forest domains (Sodré et al. 2019, Caruzo et al. 2020). The species is commonly found in the study area along trails and forest edges and roadsides in carrasco, caatinga and cerrado environments, at elevations ranging from 535 to 922 m a.s.l. (Figure 11). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 2,678,427.208 km² and Area of Occupancy (AOO) of 480.000 km².

Notes: *Croton nepetifolius* can be identified by the presence of subsessile obconic extrafloral nectaries at the apex of the petiole, leaf blades with crenate margins, with the presence of obconic extrafloral nectaries, and the abaxial face of the blade with multiradiate stellate trichomes. Its leaves have a strong odor.

Popular name: velame, marmeleiro-preto.

13. *Croton pedicellatus* Kunth (1817: 75). TYPE:—PERU. "Crescit in ripa fluminis Amazonum juxta cataractum Rentemae in Provincia Bracamorensi, alt. 200 hex.", s.d., *Humboldt s.n.* (Holotype: P) (Figure 10f, Figure 10g).

Herbs to subshrubs, 0.3–1.0 m tall, monoecious. Branches hirsute-hispid, glabrescent at maturity, with stellate, stellate-rotate, stellate-porrect, and stellate-stipitate trichomes; latex translucent. Leaves alternate, membranous; petiole 0.2–0.8 cm long, eglandular; stipules 1.0–2.2 mm long, oval, with stellate trichomes; leaf blade 0.4–0.8 × 1.8–3.6 cm, oblong to lanceolate, base attenuated to rounded, margins entire, apex mucronate, adaxial face pubescent to velutinous, with stellate, stellate-fasciculate to stellate-dendritic trichomes, abaxial face hirsute-pubescent to pubescent, with stellate to stellate-dendritic, sessile, or stipitate trichomes; venation eucamptodromous. Inflorescence 0.8–1.5 cm long, terminal, bisexual; bracts 1.0–3.0 × 0.3–0.4 mm, oval-lanceolate, hirsute-pubescent, with stellate trichomes. Staminate flower 2.0–4.0 × 2.0 mm, pedicel 1.0–2.0 mm long, receptacle hirsute to hirsute-pubescent; sepals ca. 1.8 × 1.1 mm, oval, margins entire, apex acute, external surface hirsute-pubescent, with stellate to stellate-dendritic trichomes, internal surface glabrous; petals ca. 1.2 × 0.7 mm, oblong, margins entire, apex acute, external surface hirsute to glabrous, internal surface glabrous, many trichomes concentrated along the margins; stamens 12. Pistillate flower 3.0–4.0 × 2.0–2.3 mm, pedicel 0.8–1.1 mm long, receptacle pubescent to hirsute-pubescent; sepals ca. 1.0–1.2 × 1.0 mm, oval, outer surface hirsute-pubescent, with stellate to stellate-dendritic trichomes, inner surface glabrous; petals vestigial. Ovary globose, 2.3–3.5 × 2–3.8 mm, hirsute-pubescent, with stellate trichomes; styles bifid, free from each other, with stellate trichomes. Capsule hirsute, columella with entire apex. Seed globose, ca. 2.5–3.5 × 2.5–3.5 mm, surface rough.

Selected specimens: BRAZIL. CEARÁ: Barbalha, sítio arqueológico, 18.IX.1992, fl., *L. P. Félix, 5387* (EAC); Crato, arredores da escola agrotécnica federal do Crato, 06.V.1993, *Cavalcanti FS & M. Andrade N. 33* (EAC); Crato, Chapada do Araripe, estrada casa sede, 7°14'03"S 39°24'34"W, 01.IV.1998, *L. W. Lima-Verde, et al. s.n.* (EAC); Crato, estrada Nova Olinda/Crato, Chapada do Araripe, 7°10'30"S, 39°35'27"W, 12.II.2007, *D. S. Carneiro-Torres, 868* (HUEFS).

Distribution, occurrence in the study area, and conservation status: *Croton pedicellatus* is native to the Americas, occurring in countries in South and Central America, and in Mexico (Carneiro-Torres 2009). The species is widely distributed in the northern (TO), northeastern (BA, CE, MA, PB, PI, RN, SE), midwestern (GO, MT, MS), southeastern (MG, RJ, SP), and southern (PR) states in Brazil, in Caatinga, Cerrado, and Atlantic Forest environments (Caruzo et al. 2020). It can be found

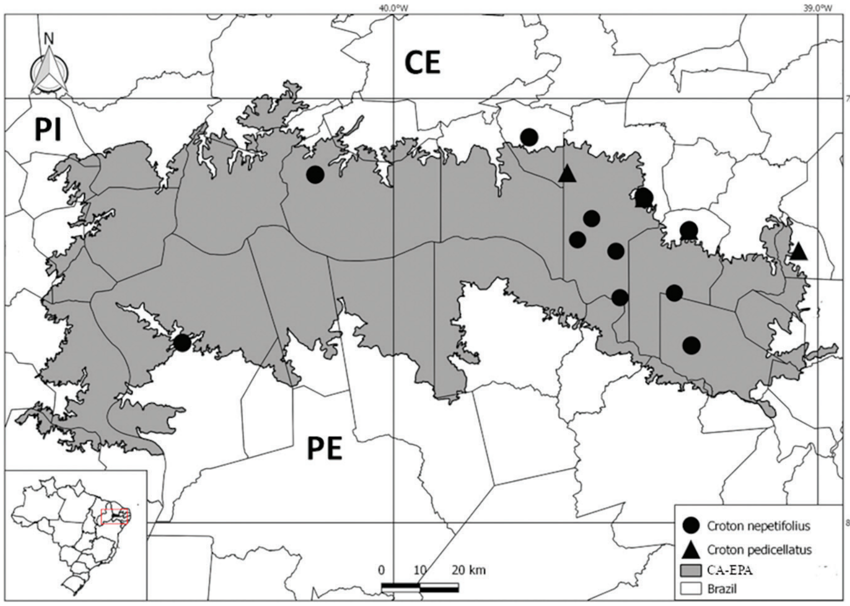

Figure 11. Distribution map of *Croton nepetifolius* and *C. pedicellatus* in the CA-EPA.

in the study area in typical caatinga and carrasco vegetations, and along roadsides (Figure 11). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 20,247,469.523 km² and Area of Occupancy of 1,476.000 km².

Notes: *Croton pedicellatus* can be distinguished from the other species by having an oblong to lanceolate leaf blade with a mucronate apex, stellate-dendritic trichomes on the external faces of the staminate and pistillate sepals and vestigial pistillate petals.

Popular name: velame, velaminho, batata-de-teiú.

14. ***Croton sertanejus*** Sodré & M.J.Silva (2022: 14–38) TYPE: BRAZIL. Bahia, Oliveira dos Brejinhos, 6 km ao Sul da cidade pela vicinal "Corredor da Barra"; 12°22′02.7″ S, 42°54′14.3″W; 884 m a.s.l.; 20/XII/2017; fl.; R.C. Sodré, A.O. Souza & U.S. Amaral 3350; (Holotype: BOTU; isotypes: CEPEC, NY, TEPB, UFG).

Shrubs, 1.5–2.0 m tall, monoecious. Branches tomentose with multiradiate to stellate-porrect trichomes; latex translucent. Leaves alternate, membranaceous, petioles 0.4–1.7 cm long, with multiradiate or stellate-porrect trichomes, 4–6 patelliform nectary glands, subsessile, stipules 0.5–0.8 × 0.15–0.3 mm, triangular, lanceolate or linear with stellate-porrect trichomes; leaf blades 2.2–8.9 × 1.2–4.7 cm, elliptic, ovate to oval-lanceolate, base obtuse or rounded, margin entire, apex acute, obtuse, mucronate to apiculate, adaxial surface hirsute, simple, stellate or stellate-porrect trichomes; venation brochidodromous. Inflorescence 2.8–16 cm long, terminal, bisexual, bracts 0.4–1.0 × 0.4–0.7 mm, triangular or oval, margins entire, apex acute, hirsute indumentum, stellate-porrect trichomes. Staminate flower 5–8 mm long; pedicel 1.6–4.7 mm long, receptacle tomentose with stellate-porrect trichomes; sepals 1.4–2.0 × 0.9–1.3 mm, ovate, fused at the base, margins entire, apex acute, external surface tomentose, with stellate porrects trichomes, internal surface glabrous; petals 2.0–2.9 × 0.6–1.2 mm, obovate, glabrous, margins entire, apex rounded, stamens 15–25. Pistillate flowers 3.5–5.3 mm long, pedicels 0.8–1.5 mm long, receptacle pubescent to tomentose, with stellate-porrect to multiradiate trichomes; sepals 1–1.7 × 0.6–0.8 mm, ovate, margins entire, apex acute, external surface pubescent to tomentose with stellate to stellate-porrect trichomes, internal surface sparsely pubescent to glabrescent; petals 0.5–1.3 × 0.5–0.4 mm, lineares, glabrous. Ovary subglobose, 1.2–1.4 × 1.3–1.8 mm, tomentose, with stellate-porrect trichomes; styles 6-fid. Capsule globose, columella with entire apex. Seed ellipsoid, 4.8–4.9 × 3–3.1 mm, with smooth surface.

Specimens examined: BRAZIL. CEARÀ: Campos Sales, Várzea da Vaca, II/1839, fl., *G. Gardner 2441* (K). PERNAMBUCO: Bodocó, arredores da cidade; 12/II/1991; fl., *P. Lisboa & C. Silva 4515, 34* (EAC).

Distribution, occurrence in the study area, and conservation status: *Croton sertanejus* is endemic to the is endemic to the Brazilian semiarid region, being recorded in the states of Bahia, Ceará, Minas Gerais, Paraíba, Pernambuco, Piauí and Sergipe, in areas of scrub/forest vegetation, sometimes associated with rocky outcrops, between 160 and 930 m. a.s.l. (Sodré & Silva, 2022); in the study area the species can be found in carrasco vegetation (Figure 12). The species was classified as Least Concern according to Sodré & Silva (2022).

Notes: As it is a recently described species, the records identified as *C. sertanejus* are still few, but we believe that the occurrence of this species in CA-EPA is not rare. *Croton sertanejus* is a recently described and illustrated species (Sodré & Silva, 2022), so it was not illustrated in the present work.

15. ***Croton suassunae*** Y. Rossine & A.L. Melo (2020: 249–253). TYPE: BRAZIL. Bahia, Rio de Contas, road to fazenda Marion, from Rio de Contas, 13°37'38"S, 41°45'25"W, 912 m, 3 Feb 2004, *Harley, R. M. et al., 54794* (Holotype: CEPEC!; isotypes: ASE, HUEFS, JPB, K) (Figure 10h).

Shrubs, 1.5–3.0 m tall, dioecious. Lepidote branches; latex not seen. Leaves alternate, chartaceous; petiole 2.0–7.0 mm long, eglandular; stipules 7 × 2 mm, lanceolate, with lepidote trichomes; leaf blade 2.0–4.3 × 1.5–2.5 cm, oval to elliptic, base rounded to chordate, margins entire, apex acute, adaxial face with stellate trichomes, abaxial face lepidote, venation eucamptodromous. Inflorescence axillary, unisexual; bracts 0.3–0.6 mm long, lanceolate, with stellate-lepidote trichomes. Staminate flower with pedicel ca. 2.0 cm long, receptacle lepidote; sepals ca. 1.3 × 3.1 mm, oval, fused at the base, margins entire, apex acute, with lepidote trichomes; petals 1.5–0.6 mm long, oblong, with simple trichomes, margins entire, apex rounded; stamens 10–15. Pistillate flower 5.0–5.2 × 4.5–5.0 mm, pedicel 1.0–3.0 mm, receptacle lepidote; sepals ca. 2.0–2.5 × 0.5 mm, spatulate, with lepidote trichomes, margins entire, apex rounded to acute; petals vestigial. Ovary globose, with lepidote trichomes; styles bifid, free. Capsule globose, columella entire. Seed ellipsoidal, surface smooth.

Specimens examined: BRAZIL. CEARÁ: Crato, 25.VI.2010, *T. R. Leite, s.n.* (HCDAL); Crato, 25.VI.2010, *T. R. Leite, s.n.* (HCDAL).

Distribution, occurrence in the study area, and conservation status: *Croton suassunae* is endemic to the Brazilian semiarid region, being recorded in the states of Bahia, Ceará, Pernambuco, and Piauí, in areas of arboreal and shrubby caatinga vegetation, cerrado, semideciduous forests, and anthropized areas (Rossine et al. 2020). The species was found in the study area in carrasco vegetation (Figure 13). The species was classified as Least Concern according to Rossine et al. (2020).

Notes: *Croton suassunae* resembles *C. argyrophyllus*, *C. limae,* and *C. tricolor*, from which it was differentiated (as described above) in *C. argyrophyllus*. As it is a recently described species, the records identified as *C. suassunae* are still few, but we believe that the occurrence of this species in CA-EPA is not rare.

16. ***Croton tricolor*** Klotzsch ex Baillon (1864:291). LECTOTYPE (designated by VanEe 2011): —BRAZIL. Minas Gerais, 1816, *A. F. C. P. Saint-Hilaire cat. C1, n. 92.* (P 00634797!) (Figure 10i, Figure 10j).

Shrubs, 1.5–2.5 m tall, monoecious. Branches glabrous to lepidote; latex translucent. Leaves simple, alternate, membranous to chartaceous; petiole 0.4–0.7 cm long, eglandular; stipules 0.4–0.9 cm long, with lepidote trichomes; leaf blade 1.5–3.2 × 3.5–10 cm, oval to lanceolate, base rounded to attenuated, margins entire, apex acute, adaxial face lepidote to glabrescent, ferruginous, with lepidote trichomes on the blade and (sometimes) stellate-porrect trichomes on the main vein, abaxial face lepidote, venation eucamptodromous. Inflorescence 1.4–9.5 cm long, terminal, bisexual; bracts 0.2–0.5 cm long, oval to lanceolate, with lepidote trichomes. Staminate flower 3.5–4.5 × 4.0–5.0 mm, pedicel 3.0–5.2 mm long, receptacle lepidote; sepals 1.8–2.8 mm, ovate, fused at the base, margins entire, apex acute, external surface lepidote, internal surface glabrous, glabrescent, or hirsute, with stellate trichomes; petals 2.0–3.0 mm, linear-lanceolate, external surface lepidote, internal

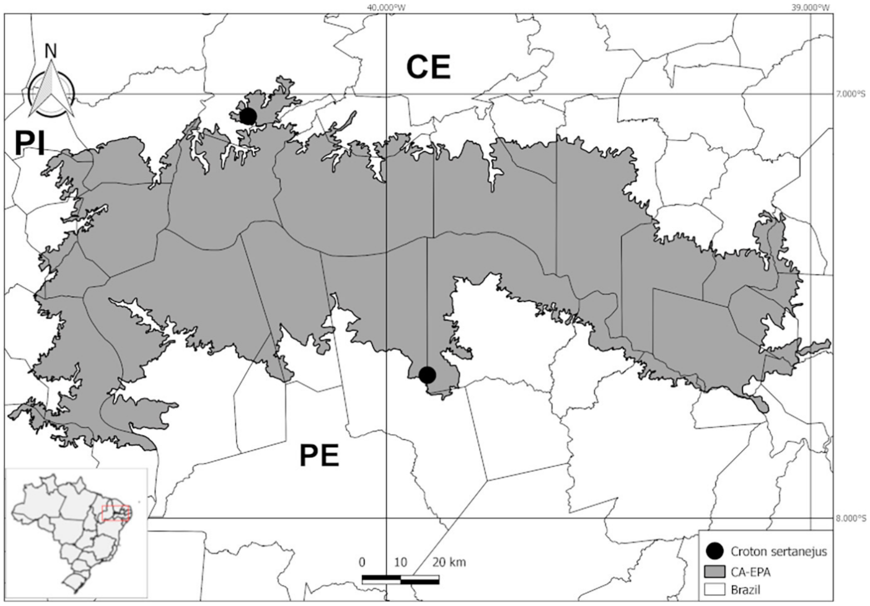

Figure 12. Distribution map of *Croton sertanejus* in the CA-EPA.

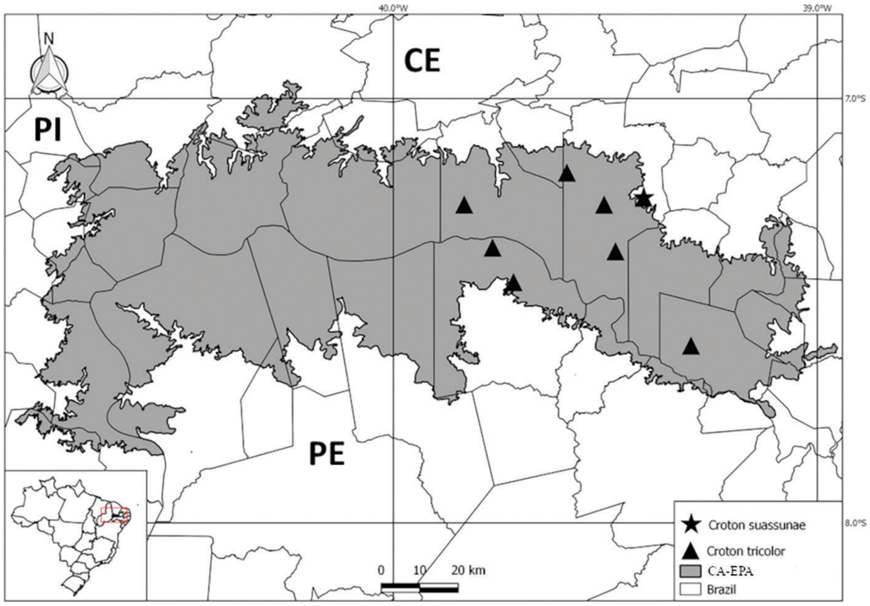

Figure 13. Distribution map of *Croton suassunae* and *C. tricolor* in the CA-EPA.

surface glabrous; 14–15 stamens, with stellate trichomes. Pistillate flower 2.8–3.0 × 5.0–6.0 mm, pedicel 2.8–3.0 mm, silvery, receptacle lepidote; sepals 0.4–0.7 cm long, oblong, margins entire, apex rounded, internal surface glabrescent, with stellate trichomes, external surface lepidote; petals absent. Ovary globose, 2–3.5 × 2–3.5 mm, with lepidote trichomes; styles multifid, with stellate trichomes. Capsule lepidote, columella with entire apex. Seed globose, 3.5–4.5 × 3.5–4.5 mm, surface smooth.

Selected specimens: BRAZIL. CEARÁ: Crato, mata úmida da FLONA, 7°14'03"S, 39°24'34"W, 11.II.2012, *C. G. Crepaldi, 57* (PEUFR); Jardim, cacimbas – FLONA, 7°34'57"S, 39°17'53"W, 09.II.2012, *C. G. Crepaldi, 42* (PEUFR). PERNAMBUCO: Moreilândia, Chapada do Araripe, Serra da Mata Grande, 7°37'51"S, 39°33'04"W, 28.IX.2016, *A. P. Fontana, 9648* (HUEFS); Exu, Chapado do Araripe, Serra do Ingá, 7°21'06"S, 39°45'58"W, 04.IV.2021, *R. M. Harley, 54161* (HUEFS).

Distribution, occurrence in the study area, and conservation status: *Croton tricolor* is native to Brazil, also occurring in other South American countries (Gomes 2006; Carneiro-Torres 2009). The species occurs in all of the states in northeastern Brazil, being also recorded in the southeastern (MG, SP) and southern (PR) regions of that country in Caatinga, Cerrado, and Atlantic Forest environments (Caruzo et al. 2020). *Croton tricolor* can be found in the study region in areas of caatinga, carrasco, and cerradão vegetation (Figure 13). The conservation status of *Croton tricolor* was previously published in the IUCN Red List (2018) as Least Concern.

Notes: *Croton tricolor* can be confused with *C. argyrophyllus*, *C. limae,* or *C. suassunae*, their differentiation was discussed in the notes concerning *C. argyrophyllus*.

Popular name: marmeleiro.

17. *Croton triqueter* Lamarck (1786: 214). SYNTYPE: —BRAZIL. Prov. Rio de Janeiro, 1767, *P. Commerson s.n.* (P00634801!, P00634800!) (Figure 10k).

Shrubs to subshrubs, 0.5–1.5 m tall. Woolly to glabrescent branches, with stellate trichomes; latex translucent. Leaves simple, alternate, membranous; petiole 0.2–6.5 cm long, pubescent, hispid to glabrescent, eglandular; stipules 0.6–1.0 cm long, entire, oval-lanceolate, with stellate trichomes; leaf blade 0.7–10.8 × 2.5–17.5 cm, oval, base rounded to truncated, margins serrate or sparsely serrate, apex acuminate, adaxial surface scabrous to glabrescent, with stellate trichomes, abaxial surface hirsute-hispid to hirsute-pubescent, with blackish stellate trichomes; venation eucamptodromous. Inflorescence 2.0–4.0 cm long, terminal, bisexual, bracts 0.6–1.2 cm long, lanceolate to linear-lanceolate, margins entire, apex acuminate, with blackish stellate trichomes. Staminate flower 3.0–4.0 × 4.0–4.2 mm, pedicel 2.3–2.5 mm long, receptacle hirsute-pubescent, with blackish stellate trichomes; sepals 2.0–3.0 mm long, oval, fused at the base, margins entire, apex acute, external surface hirsute-pubescent, with blackish stellate trichomes, internal surface glabrescent, with sparse stellate trichomes; petals 1.5–2.5 mm long, spatulate, margins entire, apex rounded, external and internal surfaces glabrescent, with sparse stellate trichomes; stamens 12. Pistillate flower ca. 0.4 × 0.5–1.2 cm, green with dark spots, pedicel 1.1–1.5 mm long, receptacle hirsute-pubescent, with blackish stellate trichomes; sepals (5 – (3 + 2)), unequal, 3 larger (ca. 3.0–4.0 mm long), oval, margins lacerated, and 2 smaller sepals, inconspicuous, external surfaces hirsute-pubescent, internal surfaces hirsute to glabrescent, with stellate to stellate-porrect trichomes; petals absent. Ovary globose, ca. 2–3 × 2–3 mm, hirsute-pubescent; styles 4-fid, fused at their base. Capsule sparsely pubescent, columella with entire apex. Seed globose, 3–4 × 3–4 mm, surface reticulate.

Specimens examined: BRAZIL. CEARÁ: Crato, Guaribas – FLONA, fl., 20.II.1999, *F. S. Cavalcanti, s.n.* (EAC). PERNAMBUCO: Exu, bacia do Rio Brígida, fazenda Mata Fresca, encosta de Chapada, 16.VII.1994, *F. S. Pinto s.n.* (EAC).

Additional specimens examined: BRAZIL. CEARÁ: Maranguape, Pó de Serra Úmida, Mucuna de Cima, 10.IV.1997, *A. S. F. Castro, s.n.* (EAC); Meruoca, Serra da Meruoca, Santo Antônio dos Fernandes, 3°34'29"S 40°29'39"W, 23.VI.2009, fl., *E. M. Marreira et al., 20* (EAC); Ubajara, Parque Nacional de Ubajara, 11.III.2014, *M. I. B. Loiola & F. R. S. Tobosa, 2200* (EAC); ALAGOAS: Palmeira dos índios, Faz, 9°21'04"S 36°40'12"W, 16.VIII.2001, fl., fr., *R. P. Lyra-Lemos, 5774* (HST).

Distribution, occurrence in the study area, and conservation status: *Croton triqueter* is widely distributed in the Neotropical region, occurring in Argentina, Bolivia, Brazil, Colombia, Mexico, Paraguay, Peru, and Venezuela (Caruzo & Cordeiro 2007; Carneiro-Torres 2009). The species occurs in the northeastern (AL, BA, CE, MA, PB, PE, RN, SE), midwestern (MS), southeastern (ES, MG, RJ, SP), and southern (PR, RS, SC) regions of Brazil, growing in Caatinga, Cerrado, Atlantic Forest, and Pantanal environments (Caruzo et al. 2020). The species was recorded in the study area in areas of humid (altered) forest (Figure 14). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 33,923,720.971 km² and Area of Occupancy (AOO) of 1,868.000 km².

Notes: *Croton triqueter* can be distinguished from the other species by having blackish stellate trichomes on the abaxial surface of the limb,

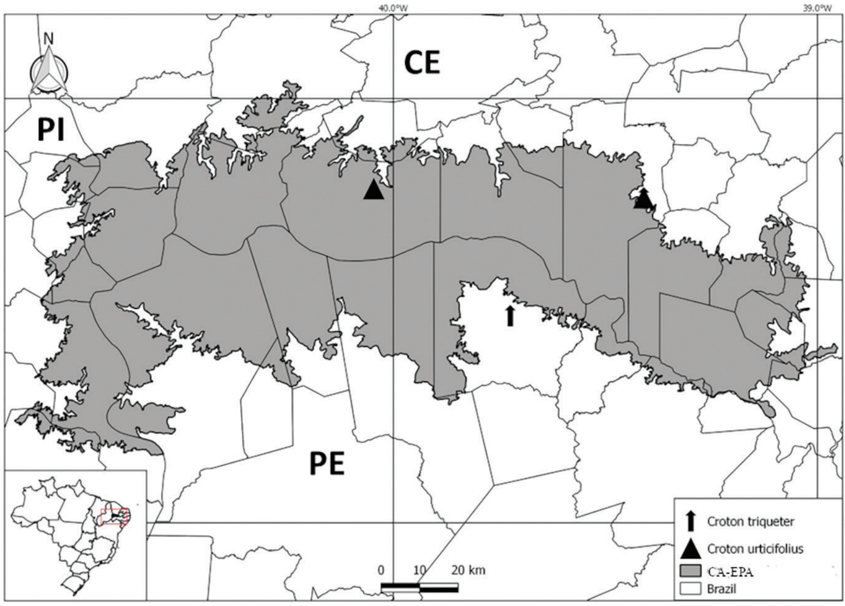

Figure 14. Distribution map of *Croton triqueter* and *C. urticifolius* in the CA-EPA.

the bracts, receptacle, and staminate sepals, as well as on the receptacle of the pistillate flower. The species can also be distinguished from the others by the sepals of the pistillate flowers of unequal size (3 larger and two smaller, inconspicuous).

Popular name: malva-da-flor-preta.

18. ***Croton urticifolius*** Lamarck (1786: 213). TYPE: —BRAZIL. Bahia, "M de Commerson a trouvè cette plante dans le Brésil (v.s.)" *Commerson, s.n*. (A) (Holotype: A) (Figure 10l, Figure 10m).

Herbs to shrubs, 0.4–2.0 m tall, monoecious. Branches hirsute, hispid to glabrescent, with stellate trichomes; latex translucent. Leaves alternate, membranous to chartaceous; petiole 0.2–2.5 cm long, with stellate to stellate-porrect trichomes, eglandular; stipules entire, elliptic; leaf blade 0.9–5.4 × 2.0–6.5 cm, oval, base oval to rounded, margins crenate to double crenate, apex acute to acuminate, adaxial surface pubescent, sparse-pubescent to glabrescent, with stellate, stellate-porrect to simple trichomes, abaxial face hirsute pubescent to tomentose, with stellate to stellate-porrect trichomes; venation actinodromous. Inflorescence 2.2–9.0 cm long, terminal, bisexual; bracts 1.1–5.0 mm long, lanceolate to oval-lanceolate, margins entire, apex acute. Staminate flower 1.3–2.5 × 1.7–3.5 mm, pedicel 0.8–2.8 mm, receptacle hirsute to glabrescent, with sparse stellate trichomes; sepals 1.0–1.7 × 0.7–1.0 mm, oval, hirsute to glabrescent; petals (5), 1.2–2.0 × 0.3–1.8 mm, oblong, margins entire, apex acute to rounded, inner and outer faces glabrescent to glabrous, with stellate trichomes; 10 stamens. Pistillate flower 3.3–4.0 × 3.0–4.0 mm, pedicel 4.0–0.8 mm long, receptacle hirsute-pubescent, with stellate to stellate-porrect trichomes; sepals 3.4–2.6 × 1.2–1.7 mm, oblong to spatulate, margins entire, apex rounded, external surface hirsute to hirsute-pubescent, with stellate to stellate-porrect trichomes, internal surface glabrous. Ovary globose, 1.5–2.1 × 1.2–2.5 mm hirsute-pubescent; styles multifid, free. Capsule pubescent, columella with entire apex. Seed oblong, 2.5–4.0 × 2.0–2.2 mm, surface rough.

Specimens examined: BRAZIL. CEARÁ: Crato, Chapada do Araripe, 7°14'03"S, 39°24'34"W, 25.II.1999, *L. W. Lima-Verde, 1301* (PEUFR); Crato, Minguiriba, Cariri, 10.I.2012, *A. C. A. Morais-Mendonça & E. N. C. Seixas, 279, 280* (HCDAL).

Additional specimens examined: BRAZIL. Ceará, Guaramiranga, Sítio Sinimbu, 4°10'30"S 38°33'21"W, 11.II.2003, *A. P. Silveira & R. F. Oliveira, 739* (EAC); Guaramiranga, Pico Alto, Sítio Gameleira, região centro-sul, 23.I.2008, fl., fr., *E. S. Rocha, s.n*. (EAC); Novo Oriente, Morro dos Três Irmãos, 20.II.1989, *F. S. Araújo, s.n.* (EAC); Ubajara, escritório do ICMBio, 3°30'11"S, 40°33'49"W, *M. I. B. Loiola et al., 1525* (EAC); Ubajara, Jaburuna/Sul, 21.II.1995, *F. S. Araújo, 1126* (EAC); Ubajara, Planalto da Ibiapaba, 27.I.1996, *A. B. Araújo, 1158* (EAC). PERNAMBUCO: Venturosa, Parque Pedra Furada, 8°34'30'S 36°52'45"W, 18.VI.1998, fl., *K. C. Costa, 46* (PEUFR).

Distribution, occurrence in the study area and conservation status: *Croton urticifolius* occurs in a number of South American countries: Bolivia, Brazil, Guyana, and Venezuela (Lucena 2001). The species has been recorded in the northern (TO), northeastern (AL, BA, CE, PB, PE, PI, RN, SE), and southeastern (ES, MG, RJ) regions of Brazil, in Caatinga, Cerrado and Atlantic Forest vegetation (Flora do Brasil 2020). The species is generally found in the study area in typical caatinga and carrasco vegetation (Figure 14). The species was classified as Least Concern in relation to its Extent of Occurrence (EOO) of 1,914,814.199 km² and Area of Occupancy (AOO) of 716.000 km².

Notes: *Croton urticifolius* can be distinguished from the other species by the presence of ten stamens in the staminate flower.

Discussion

Regarding the collection effort in the CA-EPA region, Loiola et al. (2015) related the fact that the most collected municipalities are close to university campuses, such as the Universidade Regional do Cariri, in the state of Ceará, and the Universidade Vale do São Francisco (UNIVASF) and the Serra Talhada campus of Universidade Federal Rural de Pernambuco (UFRPE-UAST) in the state of Pernambuco, the presence of these research centers in nearby regions directly influences the collection effort in these municipalities.

All the vegetation types present in the CA-EPA harbor *Croton* species – predominantly in caatinga and carrasco vegetation. *Croton heliotropiifolius* and *C. tricolor* were recorded in all vegetation types present in the CA-EPA, which corroborates the wide distribution these species present in different domains (i.e.: Caatinga, Cerrado and Atlantic Forest), not only in the Northeast region but also other regions of Brazil (Caruzo et al. 2020). In contrast, *C. betaceus* and *C. floribundus* have records only in humid forest environments, which also corroborates the distribution data for these species, as both are generally found in Amazon Rainforest and Atlantic Forest areas (Caruzo et al. 2020). The Caatinga has the highest number of endemic species among the Seasonally Dry Tropical Forest and Woodland (SDTFW), as observed for *Croton*, since this domain comprises a high diversity and endemism for the genus in Brazil (Fernandes & Queiroz, 2018).

Of the 18 species of *Croton* found in the CA-EPA, only *C. glandulosus* and *C. tricolor* are on the international list of threatened species (IUCN, 2022); in the period of the study by Loiola et al. (2015) none of the 14 *Croton* species included in the survey had information about their conservation status recorded in an online database, which highlights the lack of studies, and also of dissemination related to this theme, which ends up making it even more difficult to implementation of conservation strategies aimed at these species and the environments in which they inhabit.

In the specieslink platform (specieslink.net/search), 22 names accepted in *Croton* for the Chapada of Araripe area are listed, however in this list *C. suassunae* and *C. sertanejus* are not contemplated and, during the curse of the present work, it was elucidated that four species (*C. ceanothifolius*, *C. cerinodentatus*, *C. luetzelburgii*, *C. sclerocalyx*) were wrongly identified and do not occur in the study area. This highlights the importance of taxonomic work carried out by specialists in the groups and how it is crucial to consider that the survey, both in the field and in the herbarium, conducted with taxonomic expertise carried out by specialists, increases the chance of finding more realistic data with greater reliability in the identifications (Bebbera et al. 2010).

From a morphological point of view, the similarity between some species makes their taxonomic delimitations difficult. *Croton echioides,* and *C. sertanejus* stand out, for example, by having shrub habit, leaf blade with margins entire and extrafloral nectaries on the petiole. Easily diagnosed species, on the other hand, such as *C. floribundus*, *C. jacobinensis,* and *C. triqueter*, were also considered.

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Author Contributions

Joesili Oliveira: design, collections and visits to the herbaria, creation of the database, reading, writing and review.

Yuri Rossine: reading, writing, reviewing, correcting the manuscript.

Rayane Ribeiro: conception, co-orientation, reading, revision, correction of the manuscript.

Sarah Athiê-Souza: conception, supervision, reading, revision, correction of the text and research funding.

Conflicts of Interest

We, the authors, declare that we have no conflicts of interests related to the publication of this manuscript.

Data Availability

URL of the dataset: https://data.scielo.org/dataset.xhtml?persistentId=doi:10.48331/scielodata.JL9HLA&version=DRAFT

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Identification Key

Morphological characterization and taxonomic key for tadpoles of Brazilian Cerrado

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Abstract: Currently, amphibians are recognized as the most threatened vertebrate group worldwide. In this context, studies that offer tools for amphibian conservation are strategic to reduce the threats to this group. The absence of detailed descriptions and morphological variation of the anuran larval stage and the lack of identification tools increase the difficulty of anuran larval stage identification by non-specialists. Here we present the morphological characterization of tadpoles of 49 anuran species that occur in the Cerrado biome and transitional areas. Also, we compared our characterization with available descriptions of the tadpole and provided comments about the morphological variation found in our samples. Finally, we produced a taxonomic key as a tool for species identification using the anuran larval stage.

Keywords: *larval stage; morphology; phenotypic plasticity; taxonomy.*

Caracterização morfológica e chave taxonômica para girinos do Cerrado Brasileiro

Resumo: Atualmente, os anfíbios são considerados como o grupo de vertebrado mais ameaçado no mundo. Nesse contexto, estudos que disponibilizem ferramentas para ajudar nos esforços de conservação dos anfíbios são estratégicos para se reduzir as ameaças ao grupo. A falta de descrições detalhadas da variação morfológica das larvas de anuros e a falta de ferramentas de identificação para este estágio de desenvolvimento dificultam a atribuição correta dos táxons por não-especialistas. Nós apresentamos neste manuscrito a caracterização morfológica das larvas de 49 espécies de anuros que ocorrem no Cerrado e áreas de transição. Nós também comparamos nossa caracterização com as descrições disponíveis de girinos e discutimos sobre a variação morfológica encontrada entre os trabalhos e nossa amostra. Por fim, também aapresentamos uma chave taxonômica para uma ferramenta para a identificação de espécies de anuros utilizando o estágio larval.

Palavras-chave: *fase larval; morfologia; plasticidade fenotípica; taxonomia.*

Introduction

Amphibian populations are declining worldwide (Blaustein 2002), with almost 41% of the known species at risk of extinction (Pimm et al. 2014). Public agencies for environment management have proposed conservation programs for several species in different countries in an effort to revert the threatened status of amphibians (Mushet et al. 2012; see also the Brazilian Ministry of Environment resolutions n° 25/2012 and n° 293/2018 for example of conservation action plans for amphibians). However, the lack of basic information about species' natural history or distribution adds an extra layer of difficulty to planning conservation strategies (see a review in Brito 2010). For example, the correct identification of specimens used in several types of scientific research, from surveys to ecological experiments, is an activity that has its importance underestimated (Bortolus 2008). Errors in species identification can have unpredictable consequences for research outcomes, and the correct use of taxonomy is necessary for the estimation of species richness (e.g., Gotelli 2004, Bortolus 2008, Trindade-Filho et al. 2012, Melo et al. 2013, Rossa-Feres et al. 2015).

The negative effect of the knowledge gap in taxonomy for anuran conservation is a concern for regions such as the Brazilian savannah, due to the high rate of degradation and environmental modification, associated with high levels of endemism and diversity of amphibians (Myers et al. 2000, Bini et al. 2006, Trindade-Filho et al. 2012, Melo et al. 2014). The Brazilian Savanna, also known as "Cerrado", is the second largest Brazilian biome, being considered the largest savanna region in South America and the most diversified savanna in the world (Ab'Saber 1977, Silva & Bates 2002). Currently, about 220 species are known to this biome, with ~52% of these species considered endemic (Valdujo et al. 2012, Azevedo et al. 2016). However, this richness is probably underestimated since many new species have been described each year (e.g., Andrade et al. 2018, Pinheiro et al. 2018, Vaz Silva et al. 2018).

For most anuran species, the larval stage, denominated tadpoles, are the easiest developmental stage to encounter and to collect, since they remain in the aquatic environment for a longer period than adults, which makes them a fundamental component for biodiversity surveys (Lips & Savage 1996, Altig & McDiarmid 1999, Rossa-Feres & Nomura 2006, Andrade et al. 2007, Alves-Ferreira et al. 2021). Also, the importance of the larval traits for reconstruction of the phylogenetic relationships (e.g., Haas 2003, Frost et al. 2006) and ecological processes modelling has been increasingly recognized (see a discussion in Rossa-Feres et al. 2015). For example, morphological variation has been used for taxonomy (e.g., Rossa-Feres & Nomura 2006, Channing et al. 2016, Arifin et al. 2018, Dubeux et al. 2020, Montilla et al. 2023), ecotoxicology (e.g., Costa & Nomura 2016, Costa et al. 2017), and investigating ecological process at the community level (e.g., Marques & Nomura 2015; Marques et al. 2018; Annibale et al. 2020). However, we need to better understand the natural morphological variation of tadpoles, resulted from interaction with predators and competitors or from inter- and intrapopulation variation, to differentiate it from the impact on anurans of changes in land use, land cover, climate change, or other man-induced environmental modifications (Rossa-Feres et al. 2015). Without knowing the normal variation in each population, the association of morphological changes to anthropogenic disturbance is more challenging (Costa & Nomura 2016, Costa et al. 2017, Annibale et al. 2020). This is particularly important when we consider the actual conservation status of the Cerrado biome and its rate of habitat modification and land-use conversion, and the threats to the herpetofauna (Klink & Machado 2005, Colli et al. 2020).

Despite the growing importance of tadpoles in different branches of science, the difficulties in the correct identification of species still represents a major obstacle to include anuran larvae in management and conservation studies, mainly due to the high intraspecific morphological variation in tadpoles (Andrade et al. 2007). Also, the misleading identification of tadpoles could result in an artificial morphological variation, as variation in tadpole morphology could be a consequence of the difficulty in identifying cryptic species (Santos et al. 2018). Without an understanding of the species morphological variation throughout its area of occurrence, the interpretation of the variation among populations will remain unclear (Gehara et al. 2014). Thus, investment in the training of taxonomists, incentives for collaboration between researchers, for example, in addition to tools to increase accuracy in species identification are important actions to reduce this knowledge gap (Bortolus 2008).

One valuable tool for accessing correct species identification of anuran larvae is the use of taxonomic keys, while not the sole, taxonomic keys are highly useful and easily accessible (Gotelli 2004). Additionally, they offer a more cost-effective solution compared to other techniques (Stein et al. 2014). Despite the importance of this tool and the high anuran diversity in Brazil, only seven identification keys for tadpoles are known up-to-date: one for the region of Central Amazonia (Hero 1990), one for species occurring in the northwestern region of São Paulo state (Rossa Feres & Nomura 2006), one for the Rio Grande do Sul state (Machado & Maltchik 2007), one for species with occurrence in municipalities of Alvorada de Minas, Conceição do Mato Dentro and Dom Joaquim, Minas Gerais state (Pimenta et al. 2014), one for the southward portion of Ilha Grande, municipality of Angra dos Reis, Rio de Janeiro state (Fatorelli et al. 2018), and more recently one key for tadpoles of the northern region of the Atlantic Forest (Dubeux et al. 2020) and another for the Iron Quadrangle, Southeastern Brazil (Pezzuti et al. 2021). Here we present a characterization of the external morphology and an identification key for tadpoles of 49 species with occurrence in areas of Brazilian Cerrado (following the species inventories for the Biome presented in Valdujo et al. 2012 and Azevedo et al. 2016).

Material and Methods

1. *Study area*

Geographically, the Cerrado biome occupies a central position in South America and shares contact zones with the two largest rainforest blocks of the Neotropics (Amazonia and Atlantic Forest biomes) as well as with two dry regions (Caatinga and Chaco biomes) (Ab'Saber 1977, Silva & Bates 2002). The Cerrado is characterized by a complex landscape with high horizontal heterogeneity along its distribution, from open and savanic vegetation to forested habitats (Ribeiro & Walter 1998). The savanna formations include the "*campo rupestre*" (*sensu* Silveira et al. 2016) and "*cerrado sensu stricto*" vegetational types, also known as the typical *cerrado* (Ribeiro & Walter 1998). The forest formations are constituted of "*cerradão*" (i.e., transition between semi-deciduous forests and typical *cerrado* areas), semi-deciduous forests, "*veredas*", riparian and gallery forests (Ribeiro & Walter 1998). The grasslands formations are made up of wet grasslands, dry grasslands and "*rupestre"* fields (Campos & Lage 2013). The Cerrado biome has a strongly seasonal climate, with a wet and warm season that lasts from October to April, and a dry and cold season that lasts from May to September (Klink & Machado 2005). In this study, we used the official limits of Cerrado biome defined by the Instituto Brasileiro de Geografia e Estatística (IBGE) (available in https://www.ibge.gov.br/geociencias/informacoes-ambientais).

Valdujo et al. (2012) found that the diversity of anuran species in the Cerrado was influenced by the proximity to the surrounding domains, like the Caatinga or the Amazon. For example, they state that shared species between the Cerrado and the Amazon are less likely to co-occur with species from the Cerrado-Atlantic Forest border (Valdujo et al. 2012). The same occur for the dry diagonal (Chaco-Cerrado-Caatinga, Valdujo et al. 2012). More important, Valdujo et al. (2012) highlight the importance of transitional areas to the composition of anuran species pool in the Cerrado, especially in the transition of the Cerrado and Atlantic Forest. Thus, we included five species that occurs in transitional areas between Cerrado and Atlantic Forest, which are *Rhinella ornata x Rhinella crucifer* Thomé, Zamudio, Haddad & Alexandrino 2012, *Thoropa miliaris* (Spix 1824), *Scinax longilineus* (Lutz 1968), *Proceratophrys boiei* (Wied 1825), and *Odontophrynus* cf. *juquinha* (Baldissera et al. 2004, Valdujo *et al.* 2012, Pimenta et al. 2014, Matavelli et al. 2018, Eterovick et al. 2020). We are following Thomé et al. (2012) and citing the previous known populations of *R. pombali* Baldissera, Caramaschi & Haddad 2004 included in our samples as *Rhinella ornata x Rhinella crucifer*, once *R. pombali* is currently considered a hybrid formed by *R. crucifer* and *R. ornata* parents (Thomé et al. 2012; but see also the discussion in Pereyra et al. 2021).

2. Data collection

All tadpoles were obtained from the Coleção Zoológica da Universidade Federal de Goiás (ZUFG), municipality of Goiânia, Goiás state, Brazil (Appendix 1), collected from different localities from the Brazilian Cerrado (Figure 1). To be more concise, we present information about the collection locations along with the description of external morphology in the "Results" section. We defined the tadpole's identity using known morphological diagnostic traits with the help of ZUFG collection curators (NM Maciel, RP Bastos, and FN - one of the authors) or by consulting external experts at the time of the tadpole's collection and inclusion in the ZUFG collection (DC Rossa-Feres, W Vaz-Silva, NYN Dias – particularly for tadpoles from *Scinax*, NM Maciel – for *Rhinella*). When necessary, we also compared the morphology of tadpoles in our samples with available descriptions (indicated in the "Results" section - Comments) or by using taxonomic keys (Rossa-Feres and Nomura 2006). Following the best practices proposed by Vink et al. (2012), when we were not confident to attribute a nominal taxon for a given tadpole morphotype, but we found a consistently morphological variation that differentiates it from other species in our sample, we used "aff.", "cf.", "gr.", or "sp." as appropriate.

For the morphological characterization and elaboration of the taxonomic key, we examined two to 15 individuals between stages 30 to 40 (*sensu* Gosner 1960). For the genus *Bokermannohyla* Faivovich, Haddad, Garcia, Frost, Campbell & Wheeler, 2005, with species reproducing in lotic environments and that have longer larval period (Patterson & McLachlan 1989), we used individuals at Gosner's stage 25. Whenever possible, we included individuals from more than one population to evaluate inter-populational variation in the morphological traits. Nomenclature of morphological characteristics (Figures 2–4) followed Altig & Johnston (1986; 1989), and McDiarmid & Altig (1999). When, in the description, we were referring to the oral disc, we use "A" to describe the teeth rows that were positioned anterior to the oral aperture, and "P" to describe the teeth rows that were positioned posterior to the oral aperture. Each letter was followed by a number that represents the position of a given row of ones in relation to the oral disc, and the "A" rows follow a distal-proximal ascending order, while the "P" rows follow a proximal-distal ascending order, in relation to the oral opening, as shown in Figure 3.6 in McDiarmid & Altig (1999).

Measurements follow Altig & McDiarmid (1999) for total length (TL), body length (BL), tail muscle height (TMH), tail muscle width (TMW), spiracle length (SL), spiracle width (SW); Lavilla & Scrocchi (1986) for body height (BH), body width (BW), eye diameter (ED), nares diameter (ND), nares distance (NED); and Grosjean (2005) for dorsal fin height (DFH) and ventral fin height (VFH). All morphometric measurements shown are in millimeters. Additional measurements included the dorsal fin insertion angle, measured as acute (bellow 45-degree angle) and obtuse (equal or above 45-degree angle), and the marginal and submarginal papillae length, measured as short (when wider than longer) or long (when longer than wider).

The size classes of body shape in lateral view, nares, eye, spiracle, tail muscle, and fin height were determined by the following ratios, respectively: body width/body height (compressed $\leq 1 <$ depressed), nares size/eye diameter (small $\leq 0.14 <$ medium $< 0.38 \leq$ large $\leq 0.50 <$ very large), eye diameter/body height (small $\leq 0.17 <$ medium $< 0.29 \leq$ large), tail muscle width/body width (narrow $\leq 0.29 <$ medium $< 0.49 \leq$ wide), dorsal fin height/tail muscle height (low $\leq 0.49 <$ medium $< 1.01 \leq$ high), ventral fin height/tail muscle height (low $\leq 0.43 <$ medium $< 0.97 \leq$ high), spiracle length/body length (short $\leq 0.06 <$ medium $< 0.19 \leq$ long), and spiracle width/body height (narrow $\leq 0.09 <$ medium $< 0.25 \leq$ wide). The size classes of the above-mentioned measurements were defining as "small $\leq$ -1 SD $<$ mean $<$ +1 SD $\leq$ large" for all measurements, except for nares diameter, that was defined as "small $\leq$ -1 SD $<$ mean $<$ +1 SD $\leq$ large $\leq$ +2 SD $<$ very large", and body shape. The standard deviations for the definition of size classes were calculated considering a sample of 322 anuran Brazilian species, collected during the project "SISBIOTA Girinos do Brasil" (DC Rossa-Feres, unpublished data).

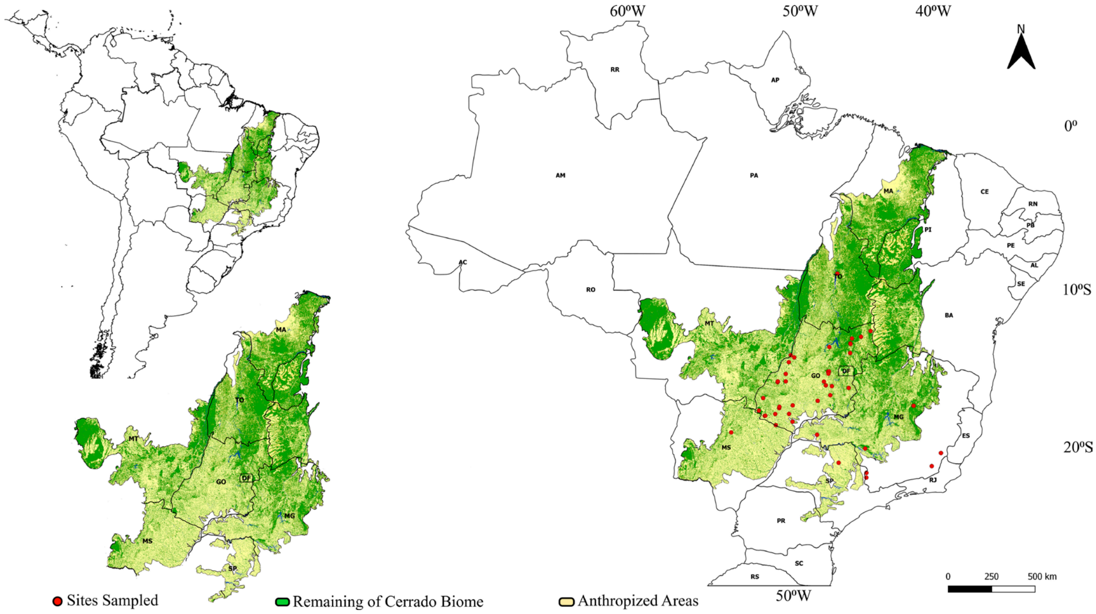

Figure 1. Map of remaining of Cerrado biome. Red circles represent the localities of the tadpoles used in the present study. Inset map: South America.

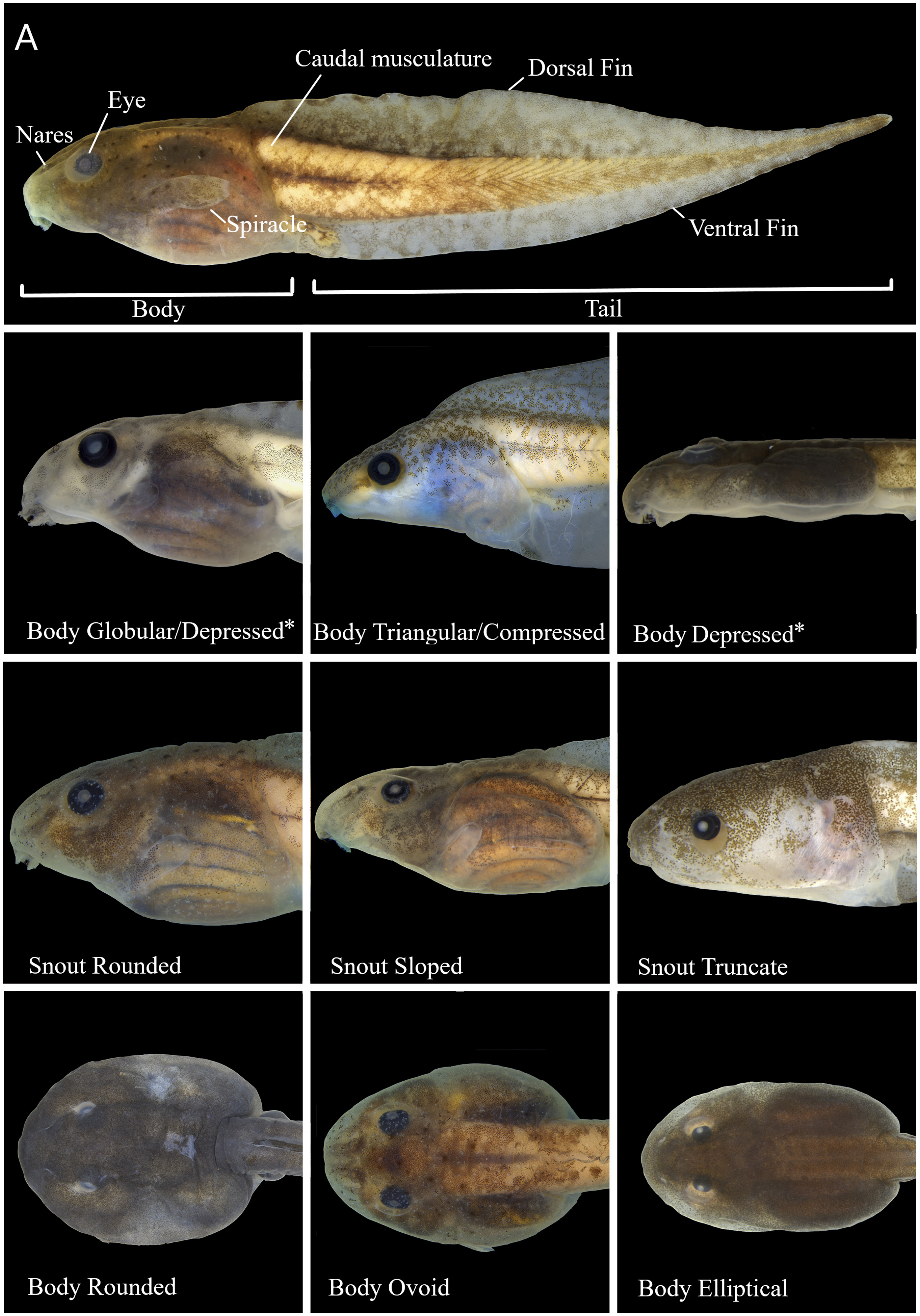

Figure 2. Morphological characteristics used to larval characterizations and in the taxonomic key. Details of a typical tadpole in lateral view, and body shape in dorsal and lateral view.

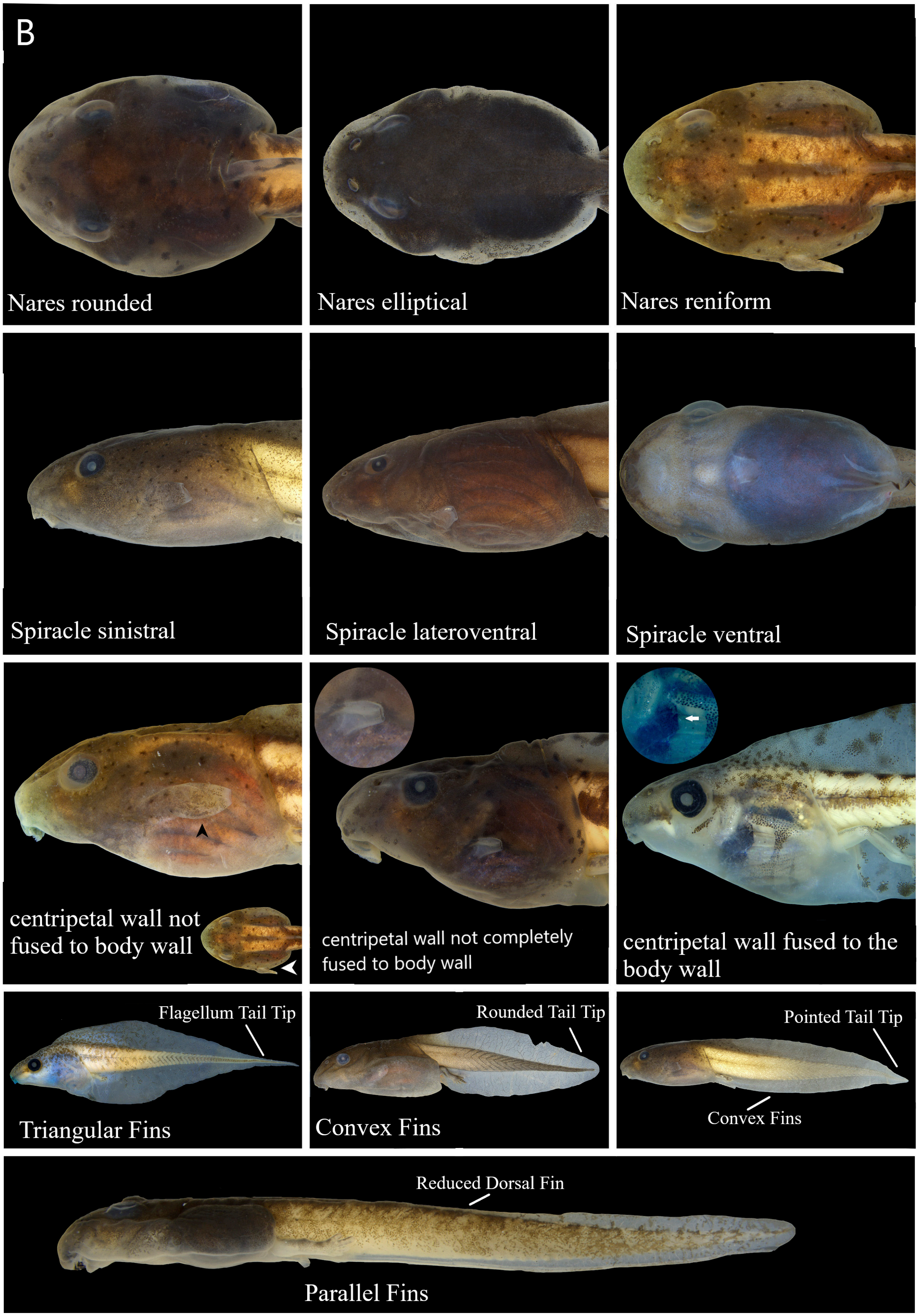

Figure 3. Morphological characteristics used to larval characterizations and in the taxonomic key. Details of the nares, spiracle, fins, and tail tips.

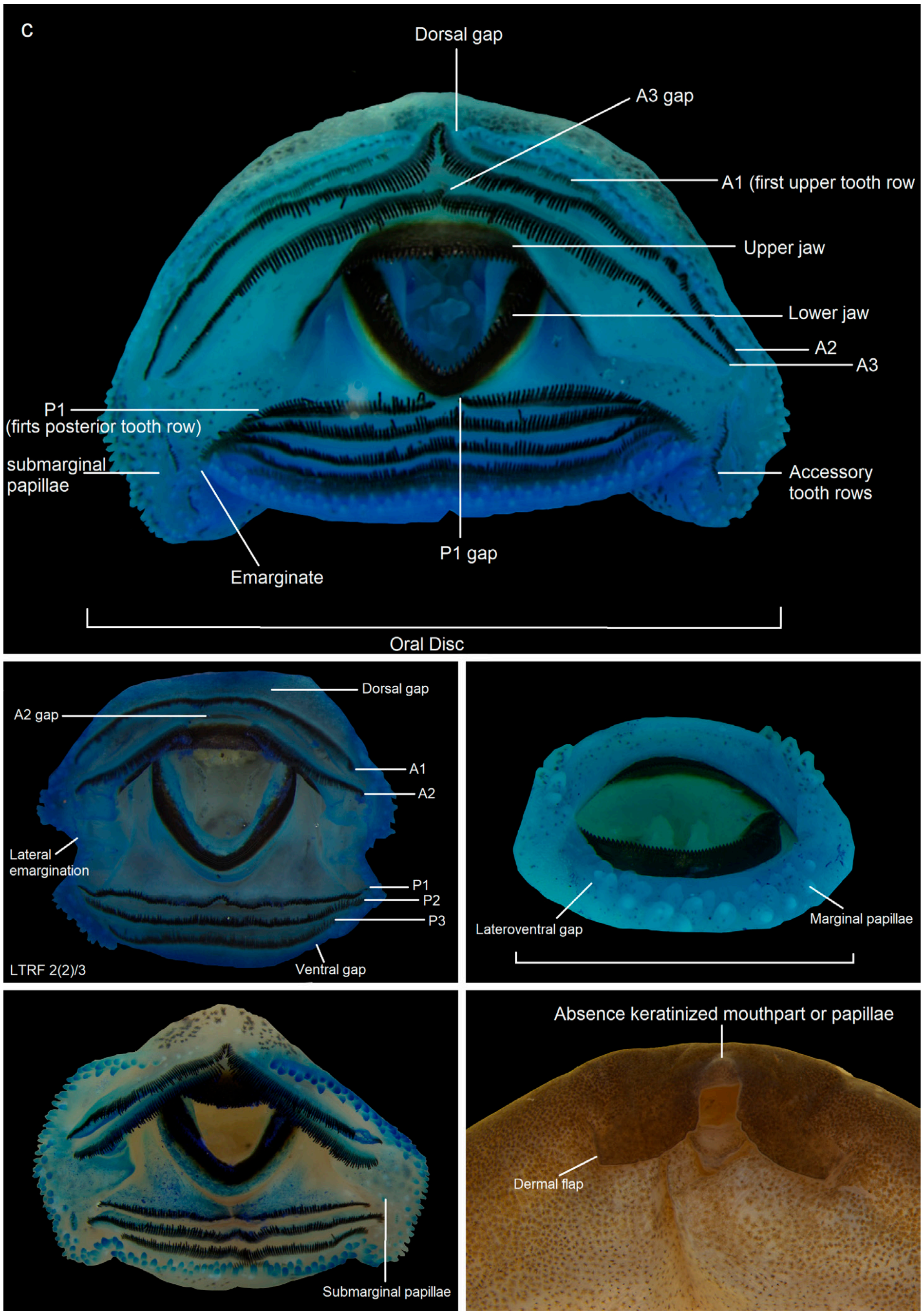

Figure 4. Morphological characteristics used to larval characterizations and in the taxonomic key. Details of the oral disc.

For body shape, we considered the body compressed when body height is higher than body width, and depressed when body width is higher than body height. Morphometric traits were reported in the characterization of each tadpole as mean ± standard deviation for total length and (range) for all other measurements. The complete morphometric information can be seen in Table 1. We considered lateral lines evident when the lateral lines were easily observed at stereomicroscopic.

All morphometric traits were measured from digital photographs, obtained with a M205A Leica® stereomicroscopic with a DFC550 camera, using the software ImageJ (1.51i). Each tadpole was placed in a petri dish and positioned in lateral or dorsal view using a water-based gel for image capture. To illustrate the external morphology, once tadpoles were larger than the visual field of the stereomicroscopic, we had taken from three to six digital images from one tadpole and combined they in an image editor software. To illustrate the oral disc, one tadpole in our series was dissected and mounted on a paraffin block, positioned with entomological pins to keep the mouth open, and submerged in distilled water for image capturing. We used a commercial 1% methylene blue solution to highlight oral disc parts, spiracle, or vent tube of tadpoles, as necessary.

Table 1. Measurements (mm) of the tadpoles characterized in this study and on which the descriptions are based on. Character abbreviations: total length (TL), body length (BL), tail muscle height (TMW), tail muscle width (TMW); body height (BH), body width (BW), eye diameter (ED), nare diameter (ND), nare-eye distance (NED); dorsal fin height (DFH), ventral fin height (VFH), spiracle length (SL), spiracle width (SW), and dorsal fin insertion angle (DFA).

Species	N		TL	BL	BH	BW	ND	ED	NED	SL	SW	DFH	VFH	TMH	TMW	DFA
Bufonidae																
Rhinella cerradensis	4	Mean	27.63	12.2	6.19	8.03	0.34	0.96	2.27	0.45	0.5	2.41	2.05	1.92	1.43	11.5
		SD	2.24	0.65	0.49	0.46	0.06	0.11	0.26	0.1	0.07	0.21	0.25	0.21	0.12	1.52
		Min	24.8	11.53	5.64	7.56	0.26	0.87	1.91	0.35	0.43	2.28	1.72	1.65	1.34	10.24
		Max	30.12	12.91	6.84	8.52	0.41	1.1	2.51	0.56	0.6	2.72	2.33	2.14	1.59	13.41
Rhinella diptycha	11	Mean	20.81	9.66	4.7	5.71	0.32	0.8	2.09	0.67	0.39	1.59	1.28	1.65	1.1	10.42
		SD	2.09	0.42	0.56	0.68	0.04	0.1	0.22	0.14	0.07	0.24	0.2	0.13	0.12	2.48
		Min	17.08	9.08	3.71	4.58	0.23	0.68	1.7	0.5	0.32	1.1	0.89	1.5	0.9	7.43
		Max	23.87	10.34	5.61	6.8	0.39	1.03	2.37	1.03	0.53	1.88	1.63	1.9	1.4	15.27
Rhinella ornata x Rhinella crucifer	4	Mean	27.97	11.63	6.6	8.29	0.29	0.93	2.29	1.07	0.76	1.78	1.55	2.18	1.73	8.13
		SD	1.86	0.89	0.53	0.49	0.06	0.03	0.1	0.11	0.07	0.44	0.35	0.1	0.12	1.31
		Min	26.32	10.77	6.02	7.65	0.2	0.91	2.18	0.97	0.68	1.28	1.11	2.03	1.55	6.72
		Max	30	12.5	7.31	8.7	0.36	0.99	2.41	1.23	0.85	2.32	1.86	2.28	1.82	9.39
Cycloramphidae																
Thoropa megatympanum	6	Mean	23.74	7.11	2.76	4.51	0.16	0.96	1.45	1.1	0.79	0.47	0.43	1.49	1.41	6.47
		SD	3.48	1.01	0.43	0.76	0.02	0.13	0.21	0.29	0.09	0.1	0.08	0.26	0.22	0.56
		Min	20.27	5.9	2.3	3.8	0.13	0.75	1.2	0.68	0.63	0.31	0.32	1.12	1.17	5.46
		Max	29.5	8.57	3.25	5.65	0.18	1.1	1.79	1.5	0.87	0.58	0.53	1.9	1.78	7.12
Thoropa miliaris	5	Mean	24.08	7.22	2.64	4.21	0.15	0.91	1.55	0.83	0.69	0.12	0.21	1.42	1.33	4.99
		SD	0.7	0.27	0.39	0.32	0.03	0.11	0.18	0.14	0.11	0.04	0.04	0.09	0.08	1.04
		Min	23.1	6.9	2.35	3.77	0.12	0.8	1.36	0.68	0.56	0.06	0.15	1.33	1.23	3.48
		Max	25.1	7.5	3.32	4.64	0.18	1.07	1.79	1.06	0.81	0.19	0.26	1.58	1.42	6.4
Dendrobatidae																
Adelphobates galactonotus	5	Mean	39.19	14.53	6.89	10.69	0.5	0.71	2.29	1.47	1.46	2	1.8	3.6	3.67	15.32
		SD	2.06	0.44	0.19	1.5	0.1	0.17	0.02	0.29	0.26	0.33	0.17	0.38	0.29	3.42
		Min	35.95	14.15	6.61	8.4	0.38	0.45	2.26	1.19	1.25	1.5	1.65	2.92	3.28	10.44
		Max	41.68	15.15	7.14	12.15	0.63	0.88	2.33	1.88	1.87	2.35	2.04	3.84	4.03	18.94
Ameerega flavopicta	5	Mean	27.06	10.99	4.88	6.55	0.17	1.05	2.22	1.09	0.85	1.59	1.11	2.56	2.61	17.15
		SD	2.84	1.12	0.21	0.66	0.01	0.13	0.13	0.18	0.17	0.21	0.24	0.38	0.3	2.08
		Min	24.47	10.21	4.58	6.07	0.16	0.9	2.03	0.95	0.67	1.41	0.89	2.37	2.31	14.72
		Max	29.95	12.57	5.06	7.54	0.18	1.21	2.32	1.37	1	1.91	1.45	3.14	2.97	19.65
Hylidae																
Boana albopunctata	15	Mean	43.93	14.39	8.5	9.87	0.58	1.66	3.46	2.1	0.98	3.06	1.86	4.43	4.38	18.23
		SD	8.04	2.03	1.5	1.64	0.1	0.26	0.58	0.57	0.2	0.58	0.41	0.96	0.91	4.42
		Min	31.6	10.55	5.75	7.13	0.41	1.22	2.73	1.3	0.68	2.22	1.14	2.87	3.02	11.01
		Max	58.98	19.35	11.7	12.82	0.71	2.15	4.39	3.28	1.42	3.79	2.48	6.1	6.17	26.56
Boana lundii	5	Mean	59.47	19.64	10.34	11.53	0.73	1.8	3.85	1.84	1.31	3.34	2.79	5.69	6.06	11.98
		SD	8.98	1.77	0.92	0.71	0.08	0.17	0.75	0.2	0.31	0.29	0.52	0.67	0.34	3.45
		Min	51.57	17.75	9	10.54	0.64	1.67	2.97	1.67	0.87	2.91	1.95	4.75	5.54	8.83
		Max	72.56	22.36	11.53	12.47	0.88	2.1	5	2.12	1.67	3.62	3.34	6.62	6.44	16.6
Boana raniceps	14	Mean	57.54	19.93	11.6	12.9	0.83	2.38	4.26	2.08	1.42	4.98	2.69	6.05	5.87	36.77
		SD	9.53	3.04	2.3	2.63	0.11	0.4	0.43	0.53	0.36	1	0.53	1	1.16	8.51
		Min	42.77	15.99	8.22	9.42	0.66	1.8	3.64	1.15	0.83	3.85	2.04	4.33	4.42	27.1
		Max	77.68	24.82	15.49	16.58	1.11	3.3	4.9	2.91	2.08	6.83	3.75	7.25	7.85	52.23

Continue...

...Continuation

Species	N		TL	BL	BH	BW	ND	ED	NED	SL	SW	DFH	VFH	TMH	TMW	DFA
Boana cf. *crepitans*	8	Mean	62.31	21.39	13.45	15.24	0.73	2.57	5.4	1.87	1.49	4.51	2.67	7	6.25	16.66
		SD	4.96	2.18	1.54	1.96	0.1	0.3	0.57	0.38	0.21	0.68	0.66	1.3	1.16	4.26
		Min	53.11	18.3	11.09	12.6	0.58	2.08	4.3	1.42	1.19	3.31	1.56	4.84	4.09	9.23
		Max	70.01	25	15.33	18.08	0.88	3.06	6	2.39	1.78	5.26	3.6	8.95	7.65	22.95
Bokermannohyla alvarengai	15	Mean	51.1	18.22	9.06	12.63	0.74	1.7	4.83	2.27	1.37	3.13	2.37	5.61	5.32	18.79
		SD	5.69	1.55	0.96	1.31	0.1	0.26	0.72	0.35	0.15	0.51	0.33	0.63	0.88	2.56
		Min	42.5	14.96	7.33	10.19	0.62	1.29	3.69	1.31	1.25	2.15	1.78	4.29	3.24	14
		Max	60.09	20.91	10.88	16.1	0.93	2.21	6	2.75	1.68	3.78	2.9	6.75	6.77	23.19
Bokermannohyla pseudopseudis	10	Mean	42.95	15	8.14	9.24	0.64	1.55	3.1	1.56	1.28	3.31	2.33	4.84	4.37	19.09
		SD	4.31	1.61	0.95	0.98	0.09	0.24	0.47	0.34	0.2	0.36	0.25	0.53	0.62	4.27
		Min	37.89	12.19	6.94	7.79	0.5	1.26	2.5	1.25	1	2.86	1.96	4.1	3.67	14
		Max	52.53	17.96	9.91	10.49	0.87	1.97	3.76	2.37	1.56	3.97	2.79	5.91	5.82	27.14
Bokermannohyla sapiranga	9	Mean	59.51	20.88	10.53	12.44	0.69	1.67	3.72	1.89	1.4	4.06	3.34	6.95	7.04	14.48
		SD	15.31	4.39	2.71	3.01	0.18	0.6	0.5	0.46	0.33	0.94	0.68	2.95	2.93	2.57
		Min	40.76	14.08	7.06	8.11	0.43	1	3.09	1.31	1.18	2.34	1.93	3.63	3.68	10.49
		Max	81.92	27.22	15.65	18.63	1	2.82	4.55	2.81	2.25	5.37	4	13.19	12.9	18.66
Dendropsophus minutus	13	Mean	34.63	11.39	6.18	6.24	0.41	1.99	3.47	0.33	0.37	3.57	4.52	3.86	3.65	28.46
		SD	5.16	1.3	0.68	0.56	0.06	0.23	0.3	0.09	0.06	0.49	0.6	0.41	0.51	7.24
		Min	27.72	9.99	5.63	5.39	0.37	1.87	2.92	0.2	0.29	2.65	3.78	3.3	3.11	16.97
		Max	42.93	13.31	7.64	6.61	0.5	2.3	4.15	0.48	0.51	4.22	5.34	4.66	3.89	42
Dendropsophus soaresi	10	Mean	36.88	11.66	6.07	6.6	0.34	1.83	3.75	0.53	0.6	3.26	3.05	4.25	3.58	23.26
		SD	1.93	0.53	0.67	0.66	0.05	0.24	0.3	0.08	0.08	0.52	0.57	0.35	0.41	5.41
		Min	32.46	10.95	5.07	5.44	0.25	1.46	3.18	0.42	0.48	2.2	2.24	3.77	3.08	15.3
		Max	39.69	12.58	6.93	7.44	0.43	2.15	4.1	0.69	0.77	3.85	3.94	4.93	4.29	33.05
Scinax fuscomarginatus	11	Mean	30.71	10.39	5.12	5.91	0.45	1.56	2.56	1.69	1.09	2.44	2.17	2.64	2.73	17.93
		SD	1.68	0.44	0.57	0.52	0.05	0.12	0.21	0.21	0.19	0.29	0.23	0.27	0.29	2.43
		Min	27.3	9.71	4.4	5.15	0.37	1.33	2.19	1.37	0.87	1.92	1.68	2.22	2.4	14.38
		Max	33.63	11.09	6.1	6.7	0.5	1.79	2.88	2	1.56	2.93	2.42	3.13	3.44	21.81
Scinax fuscovarius	12	Mean	42.13	13.85	9.35	8.59	0.68	2.38	3.79	2.07	1.44	4.14	3.32	4.8	4.52	31.29
		SD	3.76	1.18	0.83	0.72	0.07	0.23	0.32	0.29	0.32	0.62	0.9	0.69	0.54	5.36
		Min	34.89	11.04	8.49	7.49	0.56	2.09	3.38	1.62	0.75	3.33	2.51	3.97	3.86	22.22
		Max	50.7	15.42	11.07	9.92	0.81	2.73	4.38	2.5	2	5.45	5.8	6.28	5.68	38.91
Scinax longilineus	11	Mean	38.49	13.35	9.46	9.84	0.39	1.8	3.3	1.35	1.09	3.53	2.68	4.79	4.59	20.57
		SD	4.91	0.81	0.65	0.94	0.06	0.22	0.61	0.32	0.16	0.4	0.34	0.56	0.73	4.31
		Min	31.94	11.93	8.36	7.99	0.25	1.24	2.42	0.87	0.81	2.93	2.15	3.99	3.61	12.49
		Max	47.09	14.63	10.52	11.3	0.5	2.09	4.49	1.81	1.31	4.1	3.39	5.68	5.52	25.51
Scinax pombali	10	Mean	46.06	16.12	9.68	11.42	0.46	2.25	3.7	1.44	0.82	2.99	2.21	6.25	6.15	15.6
		SD	3.19	1.28	0.87	0.95	0.11	0.23	0.39	0.15	0.12	0.51	0.31	0.35	0.53	3.63
		Min	40.47	14.03	8.52	9.97	0.3	1.84	2.98	1.15	0.66	2.14	1.66	5.85	5.5	11
		Max	51.48	18.33	11.33	12.69	0.61	2.65	4.27	1.69	1.01	3.85	2.75	6.94	7.06	20.9
Scinax rupestris	11	Mean	32.04	13.91	8.81	8.82	0.22	1.97	2.45	1.44	1.26	2.79	1.89	3.49	3	15.86
		SD	3.59	1.22	0.86	0.7	0.06	0.23	0.17	0.31	0.16	0.7	0.31	0.52	0.29	2.77
		Min	24.86	12.02	7.31	7.78	0.14	1.66	2.24	0.93	0.93	1.41	1.36	2.63	2.47	12.77
		Max	37.75	16.47	9.72	9.89	0.36	2.38	2.72	1.96	1.62	3.55	2.32	4.29	3.65	19.72

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...Continuation

Species	N		TL	BL	BH	BW	ND	ED	NED	SL	SW	DFH	VFH	TMH	TMW	DFA
Scinax similis	9	Mean	30.11	10.09	6.48	6.02	0.45	1.9	2.43	1.53	0.94	3.02	2.37	3.09	3.11	24.58
		SD	2.01	1.06	0.5	0.43	0.11	0.11	0.42	0.49	0.13	0.55	0.29	0.47	0.16	8.1
		Min	27.21	9.32	5.54	5.25	0.37	1.74	1.76	1.12	0.75	2.18	1.91	2.57	2.89	15.1
		Max	33.43	12.63	7.12	6.46	0.68	2.05	3.01	2.75	1.18	3.65	2.81	4.21	3.31	36
Scinax gr. *ruber*	4	Mean	29.92	9.18	5.91	5.42	0.35	1.44	2.47	1.15	0.77	2.9	2.25	3.02	2.33	28.07
		SD	3.35	1.37	1.02	0.71	0.03	0.26	0.34	0.08	0.1	0.38	0.42	0.38	0.38	2.32
		Min	25.43	7.2	4.58	4.4	0.31	1.23	2.11	1.06	0.68	2.47	1.73	2.55	1.8	25.25
		Max	33.04	10.35	6.99	5.93	0.37	1.82	2.94	1.25	0.93	3.29	2.64	3.55	2.66	30.94
Scinax squalirostris	6	Mean	22.58	8.69	5.08	5.17	0.37	1.31	2.18	1.62	1.29	2.57	2.27	2.2	2.11	17.4
		SD	1.05	0.47	0.46	0.24	0.05	0.1	0.24	0.31	0.15	0.21	0.18	0.15	0.29	1.19
		Min	20.87	8.05	4.5	4.9	0.31	1.2	1.82	1.43	1.12	2.4	2.02	2.06	1.63	15.41
		Max	23.99	9.22	5.7	5.5	0.43	1.5	2.5	2.25	1.5	2.97	2.5	2.45	2.45	19.17
Trachycephalus typhonius	15	Mean	36.45	14.12	8.13	8.21	0.36	1.51	2.54	2.17	1.34	2.44	2.22	2.96	2.78	17.44
		SD	4.02	1.44	1.04	1	0.09	0.19	0.36	0.58	0.32	0.29	0.25	0.35	0.32	2.66
		Min	29.82	11.93	6.76	6.65	0.23	1.16	1.94	1.61	0.93	1.94	1.8	2.55	2.11	12.98
		Max	43.57	17.39	10.51	10.06	0.53	1.89	3.2	3.61	2.15	2.94	2.56	3.62	3.4	22.56
Leptodactylidae																
Leptodactylus fuscus	5	Mean	31.18	11.85	6.83	7.68	0.44	1.17	1.93	1.82	1.17	1.32	1.28	3.16	2.96	14.3
		SD	4.59	1.57	1.3	1.11	0.08	0.22	0.28	0.49	0.26	0.21	0.21	0.62	0.8	1.14
		Min	24.54	9.66	4.9	6.23	0.31	0.85	1.54	0.93	0.62	1.05	0.94	2.18	1.71	13.5
		Max	37.45	13.64	8.35	9.15	0.56	1.43	2.33	2.5	1.43	1.65	1.57	3.87	3.78	16.26
Leptodactylus labyrinthicus	15	Mean	58.71	16.94	9.99	11.69	0.56	1.65	3.46	3.14	3.25	2.24	2.16	5.68	5.36	10.21
		SD	5.13	0.98	0.54	0.78	0.04	0.22	0.41	0.51	0.34	0.34	0.26	0.4	0.42	2.15
		Min	45.83	15.79	9.23	10.62	0.5	1.32	2.69	2.06	2.7	1.69	1.79	5	4.88	6.75
		Max	65.12	19.09	11.25	13.36	0.68	1.92	4.15	4.06	3.9	2.94	2.66	6.6	6.17	13.2
Leptodactylus luctator	12	Mean	45.29	17.97	8.8	8.86	0.43	1	3.39	2.66	1.83	2.33	2.26	3.96	3.27	11.96
		SD	7.72	2.39	1.53	1.68	0.08	0.24	0.44	0.44	0.42	0.56	0.64	0.83	0.92	2.27
		Min	36.36	14.42	6.89	6.72	0.31	0.76	2.78	2.06	1.37	1.7	1.55	3.02	2.15	8.6
		Max	62.15	22.26	11.56	12.4	0.62	1.48	4.49	3.43	3	3.71	4	5.84	5.15	14.99
Leptodactylus podicipinus	3	Mean	24.02	10.26	4.85	5.7	0.33	0.7	1.95	1.18	0.89	1.58	1.35	2.19	1.91	15.61
		SD	1.08	0.39	0.07	0.18	0.03	0.14	0.1	0.28	0.24	0.16	0.09	0.15	0.17	1.64
		Min	22.83	9.88	4.77	5.51	0.31	0.55	1.85	0.87	0.75	1.39	1.27	2.09	1.79	14.3
		Max	24.95	10.66	4.92	5.87	0.37	0.83	2.06	1.43	1.18	1.69	1.46	2.38	2.11	17.45
Leptodactylus troglodytes	6	Mean	35.77	14.15	7.91	9.51	0.48	1.12	2.86	2.09	1.49	1.92	1.74	3.15	3.08	15.74
		SD	3.23	0.77	0.77	0.78	0.1	0.1	0.52	0.27	0.31	0.35	0.28	0.24	0.32	2.43
		Min	30.89	13.07	6.94	8.71	0.31	0.94	1.97	1.87	1.12	1.32	1.45	2.82	2.74	12.97
		Max	39.98	15.17	9.17	10.59	0.62	1.24	3.34	2.5	2	2.4	2.18	3.42	3.42	20.11
Physalaemus centralis	10	Mean	23.19	8.37	4.49	5.16	0.32	0.97	1.62	1.24	1.24	1.4	0.91	2.38	2.02	21.36
		SD	1.89	0.8	0.66	0.62	0.06	0.16	0.23	0.48	0.18	0.33	0.22	0.32	0.28	4.66
		Min	20.08	7.04	3.54	4.37	0.25	0.77	1.2	0.5	1	0.81	0.45	1.95	1.54	15.79
		Max	26	9.55	5.51	6.01	0.43	1.2	2	2.37	1.5	1.82	1.21	2.88	2.41	29.26

Continue...

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Species	N		TL	BL	BH	BW	ND	ED	NED	SL	SW	DFH	VFH	TMH	TMW	DFA
Physalaemus cuvieri	15	Mean	20.85	7.84	4.3	5.04	0.62	0.79	1.56	1.77	0.95	1.26	0.91	2	1.65	19.29
		SD	2.53	1.33	0.88	0.67	0.1	0.1	0.26	0.36	0.17	0.28	0.23	0.23	0.2	4.97
		Min	16.78	5.96	3.28	4.19	0.43	0.54	1.17	1.12	0.62	0.86	0.54	1.71	1.38	9.34
		Max	26.41	10.45	6.22	6.65	0.81	0.95	2.06	2.5	1.25	1.84	1.31	2.51	2.2	25.78
Physalaemus marmoratus	6	Mean	23.76	9.08	4.86	5.69	0.46	0.87	1.6	1.55	1.04	1.51	1.11	2.48	1.97	14.94
		SD	1.47	1.11	0.56	0.68	0.11	0.15	0.21	0.4	0.15	0.26	0.09	0.26	0.14	3.91
		Min	21.68	7.4	4.37	4.91	0.31	0.66	1.34	1.12	0.87	1.15	1	2.22	1.82	9
		Max	25.71	10.38	5.7	6.6	0.62	1.11	1.89	2.18	1.25	1.8	1.23	2.93	2.15	20.55
Physalaemus nattereri	13	Mean	33.84	12.68	6.9	7.96	0.44	1.14	2.16	2.22	1.2	1.96	1.34	3.3	2.55	19.09
		SD	3.1	1.19	0.74	0.82	0.11	0.19	0.55	0.48	0.18	0.38	0.29	0.4	0.43	3.27
		Min	29.9	10.64	5.35	6.51	0.31	0.75	1.15	1.25	0.81	1.33	0.74	2.53	2.01	15.18
		Max	39.95	14.17	7.99	9.47	0.7	1.42	3.15	3.06	1.56	2.57	1.68	3.86	3.4	23.86
Microhylidae																
Chiasmocleis albopunctata	6	Mean	20.25	8.5	4.93	5.34	–	1.12	1.94	1.27	1.3	1.87	1.78	1.93	1.73	19.27
		SD	2.65	0.85	0.54	0.3	–	0.14	0.11	0.22	0.33	0.48	0.5	0.33	0.35	2.58
		Min	17.52	7.79	4.18	4.99	–	0.93	1.82	0.92	1	0.97	1.18	1.92	1.35	15.88
		Max	24.14	9.82	5.82	5.89	–	1.3	2.15	1.53	1.76	2.29	2.58	2.83	2.21	23
Dermatonotus muelleri	15	Mean	36.44	15.68	8.7	11.16	–	1.47	3.8	4.02	0.82	3.13	3.13	4.3	3.47	22.18
		SD	3.61	1.37	0.92	0.94	–	0.16	0.54	0.9	0.15	0.54	0.62	0.48	0.48	4.12
		Min	29.63	13.62	7.57	10	–	1.22	2.84	2.96	0.54	2.23	2.23	3.46	2.81	15.98
		Max	41.55	17.65	10.15	12.31	–	1.85	4.93	5.02	1.04	3.57	4	4.74	4.42	29.99
Elachistocleis cesarii	15	Mean	26.94	9.04	4.59	6.39	–	0.83	2.65	1.58	0.81	1.37	1.21	2.61	2.01	25.79
		SD	4.26	0.81	0.6	0.72	–	0.1	0.31	0.28	0.17	0.15	0.3	0.34	0.34	5.04
		Min	20.81	7.83	3.75	5.45	–	0.64	2.08	1.09	0.45	1.14	0.64	2.14	1.51	18.43
		Max	36.72	10.84	5.96	8.46	–	0.95	3.24	2.1	1.05	1.59	1.7	3.36	2.87	35
Odontophrynidae																
Odontophrynus cf. *juquinha*	3	Mean	41.43	17.78	10.2	11.81	0.49	1.19	4.59	1.55	0.99	4.28	2.76	4.43	3.79	13.01
		SD	6.85	1.07	1.77	1.95	0.04	0.3	0.67	0.19	0.18	0.25	0.4	0.46	0.4	4.9
		Min	35.11	16.75	9.33	10.37	0.47	0.85	3.93	1.34	0.81	4.11	2.36	3.93	3.33	9.61
		Max	48.72	18.89	10.68	14.04	0.55	1.45	5.27	1.7	1.18	4.58	3.17	4.85	4.08	18.63
Odontophrynus cultripes	5	Mean	34.87	14.86	5.45	8.01	0.35	1.26	4.12	0.91	0.62	2.14	1.62	3.6	3.04	11.45
		SD	2.23	1.59	0.3	0.61	0.04	0.11	0.45	0.12	0.13	0.21	0.13	0.31	0.33	3.09
		Min	32.11	13.02	5.05	7.41	0.31	1.13	3.59	0.77	0.41	1.92	1.45	3.13	2.64	7.16
		Max	38.01	16.82	5.82	8.8	0.41	1.42	4.6	1.07	0.76	2.47	1.8	4.02	3.52	14.24
Odontophrynus sp.	4	Mean	53.51	22.96	14.99	16.73	0.29	2.34	5.36	2.19	1.36	5.64	4.41	5.98	5.42	10.4
		SD	2.84	1.19	1.18	0.82	0.04	0.16	0.34	0.18	0.18	0.9	0.59	0.54	0.22	1.78
		Min	50.87	21.8	13.58	15.54	0.25	2.16	4.93	1.99	1.24	4.38	3.67	5.38	5.09	8.55
		Max	57.26	24.19	16.41	17.41	0.35	2.5	5.75	2.38	1.63	6.48	5.09	6.67	5.58	12.32
Proceratophrys boiei	3	Mean	32.38	13.18	7.64	8.2	0.49	1.2	2.32	1.24	0.72	2.71	2.01	2.78	2.53	15.9
		SD	0.54	0.36	0.34	0.44	0.04	0.1	0.13	0.03	0.11	0.14	0.04	0.02	0.13	3.15
		Min	31.93	12.93	7.39	7.77	0.46	1.12	2.17	1.21	0.59	2.62	1.96	2.75	2.43	12.27
		Max	32.99	13.6	8.04	8.65	0.55	1.32	2.41	1.27	0.82	2.88	2.04	2.8	2.69	17.81

Continue...

...Continuation

Species	N		TL	BL	BH	BW	ND	ED	NED	SL	SW	DFH	VFH	TMH	TMW	DFA
Proceratophrys cururu	15	Mean	33.09	12.98	6.43	8.99	0.27	1.36	3.58	0.97	0.68	1.97	1.41	3.45	2.85	15.69
		SD	6.69	2.12	1.05	1.47	0.04	0.16	0.56	0.34	0.19	0.38	0.5	0.54	0.57	4.42
		Min	18.89	8.61	4.58	6.39	0.17	1.12	2.51	0.44	0.25	1.3	0.78	2.17	1.57	7.71
		Max	44.29	15.51	8.08	11.46	0.35	1.68	4.56	1.96	0.88	2.66	2.83	4.02	3.57	23
Proceratophrys dibernardoi	3	Mean	29.75	11.14	5.08	7.69	0.17	1.06	3.06	0.56	0.42	1.71	1.31	3.21	2.9	13.7
		SD	1.52	0.78	0.42	0.49	0.02	0.05	0.46	0.2	0.16	0.08	0.04	0.1	0.21	4.51
		Min	28.82	10.32	4.69	7.14	0.15	1	2.76	0.36	0.24	1.66	1.27	3.12	2.66	9.03
		Max	31.52	11.89	5.53	8.1	0.2	1.11	3.59	0.76	0.54	1.81	1.36	3.33	3.04	18.04
Proceratophrys salvatori	6	Mean	29.83	12.79	6.73	8.29	0.25	1.36	2.54	0.72	0.51	2.57	1.43	2.96	2.6	8.19
		SD	1.9	0.47	0.63	0.87	0.04	0.15	0.39	0.2	0.15	0.25	0.21	0.25	0.18	1.49
		Min	27.67	11.94	5.89	6.78	0.2	1.16	1.94	0.51	0.33	2.17	1.14	2.61	2.27	6.43
		Max	32.62	13.26	7.73	9.19	0.32	1.57	2.92	1.09	0.77	2.86	1.62	3.33	2.77	10.08
Proceratophrys cf. *goyana*	11	Mean	35.55	14.17	7.14	8.14	0.41	1.35	2.51	0.83	0.6	2.51	1.52	3.66	3.81	12.02
		SD	3.83	1.2	0.88	0.69	0.06	0.18	0.35	0.12	0.12	0.33	0.22	0.48	0.41	4.39
		Min	30.95	12.56	5.79	7.08	0.32	1.09	2	0.64	0.43	1.74	1.22	2.9	3.15	6.65
		Max	43.79	16.34	8.72	9	0.54	1.68	3.02	0.98	0.82	2.87	1.89	4.55	4.45	20.04
Proceratophrys sp.	5	Mean	27.54	10.19	4.57	5.43	0.61	0.77	1.7	1.38	0.97	1.74	1.27	2.4	2.09	22.57
		SD	4.99	1.78	0.95	1.32	0.11	0.11	0.27	0.19	0.14	0.25	0.25	0.59	0.78	3.43
		Min	20.34	7.8	3.26	3.98	0.5	0.62	1.46	1.12	0.81	1.37	1.03	1.69	1.37	19
		Max	32.77	11.71	5.62	7.01	0.81	0.91	2.1	1.56	1.12	2.09	1.63	3.09	2.98	27.94
Phyllomedusidae																
Pithecopus azureus	15	Mean	48.78	15.48	8.66	8.03	0.44	2.4	2.91	1.04	1.21	1.43	3.2	4.66	4.07	12.82
		SD	4.97	1.5	0.82	0.95	0.14	0.3	0.25	0.21	0.17	0.48	0.59	0.56	0.6	2.05
		Min	39.38	12.42	7.4	6.15	0.16	1.91	2.45	0.74	0.93	1.03	2.11	3.68	3.05	9.21
		Max	57.13	17.87	10.39	9.66	0.66	3.15	3.5	1.54	1.67	2.5	4.25	5.84	4.91	16.68
Pithecopus oreades	8	Mean	48.71	15.85	9.29	9.13	0.62	2.35	3.5	1.26	1.22	2.02	3.3	4.91	4.36	12.28
		SD	2.31	0.79	0.73	0.39	0.07	0.12	0.32	0.25	0.2	0.18	0.47	0.39	0.35	3.15
		Min	46.68	15.08	8.25	8.76	0.5	2.16	3.1	0.82	0.9	1.66	2.46	4.29	3.97	9.35
		Max	53.93	17.12	10.14	9.95	0.66	2.54	3.99	1.62	1.5	2.22	3.9	5.59	5.04	19.19
Pithecopus sp.	2	Mean	42.1	15.63	7.9	7.01	0.33	2.53	2.92	0.85	1.02	1.09	2.06	5.06	4.11	6.93
		SD	0.79	0.39	0.54	1.14	0	0.18	0.09	0.1	0.21	0.08	0.31	0.72	0.87	1.32
		Min	41.54	15.35	7.52	6.2	0.2	2.4	2.86	0.78	0.87	1.03	1.84	4.55	3.49	6
		Max	42.66	15.91	8.29	7.82	0.2	2.66	2.99	0.93	1.18	1.15	2.28	5.57	4.73	7.87

Results

In this study, we present the morphological characterization for tadpoles of 49 anuran species, with about 600 specimens analyzed, from the families Bufonidae (*Rhinella cerradensis*, *R. diptycha*, *R. ornata* x *R. crucifer*), Cycloramphidae (*Thoropa megatympanum, T. miliaris*), Dendrobatidae (*Adelphobates galactonotus, Ameerega flavopicta*), Hylidae (*Boana albopunctata, Boa. lundii, Boa. raniceps, Boa.* cf. *crepitans, Bokermannohyla alvarengai, Bok. pseudopseudis, Bok. sapiranga, Dendropsophus minutus, D. soaresi, Scinax fuscomarginatus, S. fuscovarius, S. longilineus, S. pombali, S. rupestris, S. similis, Scinax* sp.*, S. squalirostris, Trachycephalus typhonius*), Leptodactylidae (*Leptodactylus fuscus, L. labyrinthicus, L. luctator, L. podicipinus, L. troglodytes, Physalaemus centralis, P. cuvieri, P. marmoratus, P. nattereri*), Microhylidae (*Chiasmocleis albopunctata, Dermatonotus muelleri, Elachistocleis cesarii*), Odontophrynidae (*Odontophrynus americanus, O. cultripes, Odontophrynus* sp.*, Proceratophrys boiei, P. cururu, P. dibernardoi, P. salvatori, P.* cf. *goyana, Proceratophrys* sp.), and Phyllomedusidae (*Pithecopus azureus, P. oreades, Pithecopus* sp.), which represents about 22% of the known anuran species for the Cerrado biome. We organized this morphological information in a taxonomic key and produced a tool to help in anuran surveys and management studies in the Cerrado biome.

1. Bufonidae Gray 1825

Rhinella cerradensis Maciel, Brandão, Campos & Sebben 2007

First Description of the tadpole: Brasília – DF, Brazil (Maciel et al. 2007).

Other characterizations: Not available.

Specimens Examined: Brazil, Goiás State, municipality of Cristianópolis (ZUFG 1769). Description based on four tadpoles between Gosner Stages 36 and 37.

Characterization. Total length 27.63 ± 2.24 mm (Table 1, Figure 5). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.24–1.34). The snout is sloped in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of elongated marginal papillae, interrupted by dorsal and ventral gaps; few submarginal papillae scattered laterally, smaller than the marginal papillae. Labial teeth row formula (LTRF) is 2(2)/3(1), with row A1 = A2, P1 = P2 and P3 slightly smaller than P2 in length. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the upper jaw sheath is slightly wider than the lower jaw sheath. Nares medium (ND/ED = 0.30–0.37), elliptical, with a small projection on the marginal rim, dorsally positioned. Eyes small (ED/BH = 0.15–0.16), dorsally positioned. Spiracle sinistral, short (SL/BL = 0.03–0.04), narrow (SW/BH = 0.08–0.09), with opening at the middle third of the body, directed posterodorsally, with the centripetal wall fused to the body wall. Vent tube medial, fused with the ventral fin. The caudal musculature width is narrow (TMW/BW = 0.18–0.19). The dorsal fin is high (DFH/TMH = 1.27–1.38), originating at the body-tail junction with acute slope, and convex margin; ventral fin is high (VFH/TMH = 1.04–1.09) with convex margin; the tail tip is rounded. Lateral lines are evident.

Comments. According to Maciel et al. (2007) the tadpoles of *R. cerradensis* can be differentiated from tadpoles of other *Rhinella* species by body proportions (in relation to tail and total length), spiracle position, and the "absence of an external spiracular tube'', with the opening in the body wall. *Rhinella cerradensis* tadpoles analyzed in this study closely resemble the individual described by Maciel et al. (2007), but presented an external spiracular tube, like other *Rhinella* species. We examined the tadpoles used in the description of *R. cerradensis* (CHUNB 49574) and the absence of an external spiracular tube (Maciel et al. 2007) represents a difference in the interpretation of the authors and not a morphological variation.

Rhinella diptycha (Werner 1894)

First Description of the tadpole: Jaboticabal – SP, Brazil (Rosa, 1965).

Other characterizations: São José do Rio Preto – SP, Brazil (Vizotto 1967); Argentina (Cei 1980); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Eastern Region of the Meridional Espinhaço Range – MG, Brazil (Pimenta et al. 2014); Bahia State, Brazil (Mercês et al. 2009); Fernando de Noronha – PE, Brazil (Tolledo & Toledo 2010); northern region of the Atlantic Forest (Dubeux et al. 2020).

Specimens Examined: Brazil, Goiás State, municipalities of Aparecida do Rio Doce (ZUFG 1770), Aporé (ZUFG 1030), Portelândia (ZUFG 120), São Domingos (ZUFG 1771). Description based on 11 tadpoles between Gosner Stages 35 and 39.

Characterization. Total length 20.82 ± 2.10 mm (Table 1, Figure 6). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.21–1.23). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of conical marginal papillae, interrupted by dorsal and ventral gap; few submarginal papillae scattered laterally, smaller than the marginal papillae. LTRF is 2(2)/3, with row A1 = A2, P1 = P2 and P3 slightly smaller than P2. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the upper jaw sheath is slightly wider than the lower jaw sheath. Nares medium to large (ND/ED = 0.34–0.38), elliptical, with a small projection on the marginal rim, dorsally positioned. Eyes medium (ED/BH = 0.18–0.18), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.06–0.10), narrow (SW/BW = 0.09–0.09), opening at the middle third of the body, directed posterodorsally, with the centripetal wall completely fused to the body wall. Vent tube medial, fused with the ventral fin. The caudal musculature width is narrow (TMH/BW = 0.20–0.21). The dorsal fin has medium height (DFH/TMH = 0.73–0.99), originating at the anterior third of the tail with an acute slope, and with convex margin; ventral fin has medium height (VFH/TMH = 0.59–0.86) with convex margin; the tail tip is rounded. Lateral line not evident.

Comments. Tadpoles from populations currently associated with Rhinella diptycha were described by Rosa (1965), Vizotto (1967), Cei (1980) (as *Bufo paracnemis*), Mercês et al. (2009), Tolledo & Toledo (2010) and Dubeux et al. (2020) (as *Rhinella jimi*). Tadpoles described by Cei (1980) were larger than those used in our description. In Stage 37 the Argentinean populations presented total length of 35 mm, while the analyzed in this study at the same stage presented total length of 23.87 mm, like those described by Vizotto (1967) that presented 23.50 mm, and by Rossa-Feres & Nomura (2006) with 24.31 mm. The LTRF 2(2)/3 was the mostly common observed by us and is the same as reported by

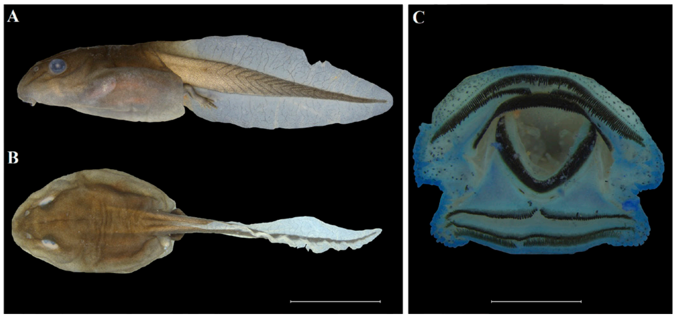

Figure 5. Tadpoles of *Rhinella cerradensis* at Stage 37 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 34 (scale 2 mm).

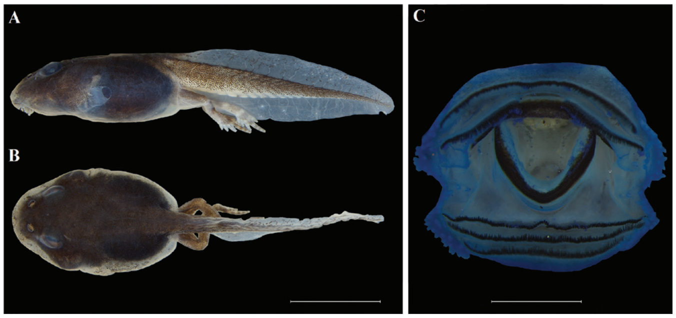

Figure 6. Tadpoles of *Rhinella diptycha* at Stage 40 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

Rossa-Feres & Nomura (2006), Mercês et al. (2009), Tolledo & Toledo (2010) and Dubeux et al. (2020), differing from the LTRF 2(2)/3(1) described by Rosa (1965), Vizotto (1967) and Cei (1980). Both Rosa (1965) and Rossa-Feres & Nomura (2006) suggests that the interrupted P1 could be caused by manipulation of the tadpoles, but this seems instead morphological variation. From the eleven tadpoles analyzed, two presented the P2 slightly wider than P1, two individuals from different locations presented the LTRF 2(2)/3(1) and the submarginal papillae with the same size of the marginal papillae. *Rhinella diptycha* seems to have variable spiracle position among the different populations studied. In Rossa-Feres & Nomura (2006), the position of the spiracle is in the posterior third of the body, while in Cei (1980) and Tolledo & Toledo (2010) the spiracle is described as positioned at the midbody, while Mercês et al. (2009) described it as positioned in the anterior half of the body. Dubeux et al. (2020) do not provide a description for *R. diptycha* but informs its general aspects together with other *Rhinella* tadpoles included in their study. In our samples, five individuals in both lots analyzed had the spiracle positioned at the posterior third of the body. Tadpoles of *R. diptycha* can be distinguished from *R. cerradensis* by having the body elliptical in dorsal view, depressed body, dorsal fin originating at the anterior third of the tail, LTRF 2(2)/3, mainly by snout rounded in lateral view, and by the presence of unpigmented longitudinal stripe along the ventral edge of the tail musculature.

Rhinella ornata x Rhinella crucifer Thomé, Zamudio, Haddad & Alexandrino 2012

First Description of the tadpole: Catas Altas – MG, Brazil (Lourenço et al. 2010).

Other characterizations: Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014); Iron Quadrangle region (Pezzuti et al. 2021).

Specimens Examined: Brazil, Minas Gerais State, municipality of Cataguases (ZUFG 2352). Description based on four tadpoles at Gosner Stage 40.

Characterization. Total length 27.97 ± 1.87 mm (Table 1, Figure 7). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.19–1.27). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of conical marginal papillae, interrupted by dorsal and ventral gap; few submarginal papillae laterally, forming a row on the inner side of the lateral emargination, with the same size as the marginal papillae. LTRF is 2(2)/3, A1 = A2, P1 = P2 and P3 slightly smaller than P-2; the upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the upper jaw sheath slightly wider than the lower jaw sheath. Nares medium (ND/ED = 0.22–0.36), elliptical, with a small projection on marginal rim, dorsally positioned. Eyes small (ED/BH = 0.14–0.15), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.09–0.10) and medium width (SW/BH = 0.11–0.12), opening at the middle third of the body, directed posterodorsally, with the centripetal wall completely fused to the body wall. Vent tube medial, fused with the ventral fin. The caudal musculature width is narrow (TMW/BW = 0.20–0.21). The dorsal fin has medium to high height (DFH/TMH = 0.63–1.02), originating at the body-tail junction with acute slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.55–0.82) with convex margin; the tail tip is rounded. Lateral line not evident.

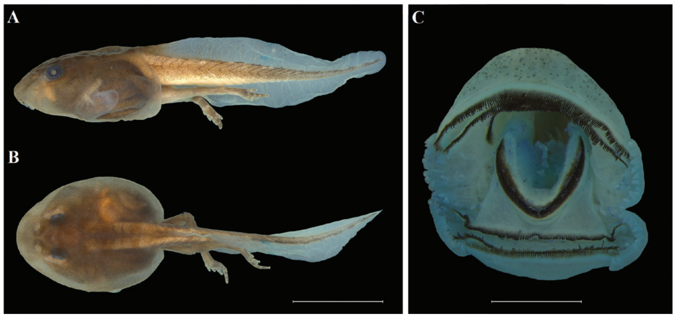

Figure 7. Tadpoles of *Rhinella ornata x Rhinella crucifer* at Stage 40 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

Comments. *Rhinella pombali*, treated as a species by Baldissera et al. (2004), is currently considered a hybrid formed by *R. crucifer* and *R. ornata* parents (Thomé et al. 2012; but see also the discussion in Pereyra et al. 2021). Thus, we used previous descriptions of tadpoles treated as *R. pombali* to compare with our description. The populations analyzed by Pimenta et al. (2014), treated as *Rhinella crucifer* were compared to our description. The populations described by Lourenço et al. (2010) were smaller (total length = 21.50 mm) than the populations that we studied, but this difference could be explained by the difference in the developmental stages of the tadpoles analyzed [stages 35–38 in Lourenço et al. (2010), stage 40 in our sampled population]. In addition, the tadpoles describe by Lourenço et al. (2010) have the oral disc not emarginate, but the figure shows that the oral disc is emarginate laterally. We found intrapopulation variation in teeth row formula, with one individual with LTRF 2(2)/3(1), and in submarginal papillae, with one individual without submarginal papillae. Tadpoles of (formerly known as) *R. pombali* can be distinguished from tadpoles of *R. cerradensis* by the rounded snout, and LTRF 2(2)/3, and from tadpoles of *R. diptycha* by the ovoid body shape, larger body proportions, eyes dorsolaterally directed, and spiracle opening at the posterior third of the body.

2. Cycloramphidae Bonaparte 1850

Thoropa megatympanum Caramaschi & Sazima 1984

First Description of the tadpole: Serra do Cipó – MG, Brazil (Caramaschi & Sazima, 1984).

Other characterizations: Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014); Iron Quadrangle region (Pezzuti et al. 2021).

Specimens examined: Brazil, Minas Gerais State, Parque Nacional de Sempre Vivas (ZUFG 927). Description based on six tadpoles between Gosner Stages 35 and 37.

Characterization. Total length 23.70 ± 3.48 mm (Table 1, Figure 8). The body shape is ovoid in dorsal view and oval-depressed in lateral view (BW/BH = 1.65–1.73). The snout is rounded in lateral view. The oral disc is ventral, lateroventrally emarginate, with a uniseriate row of marginal papillae, elongated laterally and short ventrally, interrupted by a dorsal gap; submarginal papillae absent. The LTRF is 2(2)/3, A1 = A2, P1 = P2 and P3 slightly smaller than P-2. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is wide, U-shaped; the lower jaw sheath is wider than the upper jaw sheath. Nares medium (DMN/DMO = 0.16–0.17), elliptical, laterally positioned. Eyes

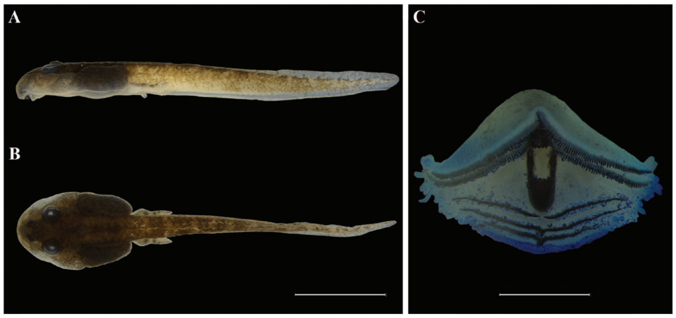

Figure 8. Tadpoles of *Thoropa megatympanum* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

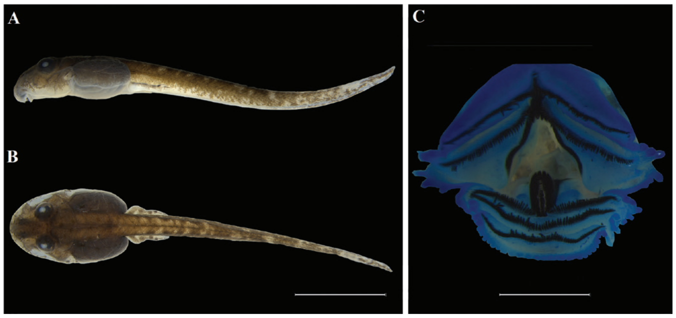

Figure 9. Tadpoles of *Thoropa miliaris* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

large (ED/BH = 0.33–0.34), dorsally positioned. Spiracle sinistral, lateroventral, with medium length (SL/BL = 0.12–0.18), wide (SW/BH = 0.27–0.27), opening at the middle third of the body, directed posterodorsally, with the centripetal wall completely fused to the body wall. Vent tube medial, with free distal edge. The caudal musculature width is medium (TMW/BW = 0.31–0.32). The dorsal fin is low (DFH/TMH = 0.27–0.30), originating at the middle third of the tail with acute slope, and parallel margin; ventral fin is low (VFH/TMH = 0.27–0.28) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line not evident.

Comments. The tadpoles from Sempre Vivas National Park were like those described by Caramaschi & Sazima (1984), but the populations described by Pimenta et al. (2014) and Pezzuti et al. (2021) differ due to the vent tube fused to the ventral fin. From the total of analyzed individuals, two have the A1 slightly smaller than A2, two presented LTRF 2(1,2)/3(1), and one LTRF 2(2)/3(1).

Thoropa miliaris (Spix 1824)

First Description of the tadpole: Cubatão – SP, Brazil (Bokermann, 1965).

Other characterizations: Iron Quadrangle region (Pezzuti et al. 2021).

Specimens Examined: Brazil, Minas Gerais State: Cataguases (ZUFG 2342). Description based on five tadpoles at Gosner Stage 39.

Characterization. Total length 24.09 ± 0.71 mm (Table 1, Figure 9). The body shape is elliptical in dorsal view and oval-depressed in lateral view (BW/BH = 1.30–1.60). The snout is rounded in lateral view. The oral disc is ventral, ventrally emarginate, with a uniseriate row of marginal papillae, elongated laterally and short ventrally, interrupted by dorsal gap; submarginal papillae absent. LTRF is 2(2)/3(1), A1 = A2, P1 = P2 > P3. The upper jaw sheath is wide, arc-shaped, and the lower jaw sheath is wide, U-shaped; the upper and lower jaw sheath of the same width. Nares medium (ND/ED = 0.15–0.17), elliptical, laterally positioned. Eyes large (ED/BH = 0.32–0.34), dorsally positioned. Spiracle lateroventral, with medium length (SL/BL = 0.10–0.14) and width (SW/BH = 0.24–0.24), with opening at the middle third of the body, directed posterodorsally, with the centripetal wall completely fused to the body wall. Vent tube medial, with free distal edge. The caudal musculature width is medium (TMW/BW = 0.31–0.31). The dorsal fin is low (DFH/TMH = 0.05–0.12), originating at the posterior third of the tail with acute slope, and margin parallel to the caudal musculature; ventral fin is low (VFH/TMH = 0.11–0.16) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line not evident.

Comments. Tadpoles analyzed in this study are like the description of Bokermann (1965) and Pezzuti et al. (2021), and just one individual in our sample had a different LTRF of 2(1,2)/3(1). Pezzuti et al. (2021) described the tadpoles with the oral disc lateroventrally emarginate, while we considered the emargination ventral, with a small nostril, while we considered the nares medium sized, and with a short spiracle, while we considered it medium sized. Tadpoles of *T. miliaris* can be distinguished from tadpoles of *T. megatympanum* by the elliptical body in dorsal view, lower dorsal fin, and larger vent tube (LT/LMC = 1.72 mm in *T. miliaris*, and LT/LMC = 1.27 mm in *T. megatympanum*). However, regarding this last trait, we suspected that the vent tube in our *T. miliaris* sample were damaged during collecting and the validity of this difference should be evaluated in future studies.

3. Dendrobatidae Cope 1865

Adelphobates galactonotus (Steindachner 1864)

First Description of the tadpole: Araguaína – TO, Brazil (Santos et al. 2018).

Other characterizations: Not available.

Specimens Examined: Brazil, Tocantins State, municipality of Araguaína (ZUFG 2508).

Characterization. The following information is complementary to the description available in Santos et al. (2018). Total length 39.19 ± 2.07 mm (Table 1, Figure 10). The body shape is globular-depressed in lateral view (BW/BH = 1.27–1.70), nares very large (ND/ED = 0.72–0.84), eyes small (ED/BH = 0.07–0.12), spiracle medium-sized (SL/BL = 0.08–0.12) and medium width (SW/BH = 0.19–0.26). The caudal musculature width is medium (TMW/BW = 0.33–0.39), and the dorsal (DFH/TMH = 0.51–0.61) and ventral (VFH/TMH = 0.53–0.57) fins have medium height.

Comments. A discussion about the importance of larval morphology for systematic of the Dendrobatoidea and their relatives was provided by Santos et al. (2018).

Ameerega flavopicta (A. Lutz 1925)

First Description of the tadpole: Santana do Riacho – MG, Brazil (Haddad et al. 1994).

Other characterizations: Serra de Caldas State Park – GO, Brazil (Costa et al. 2006); Jaboticatubas– MG, Brazil (Dias et al. 2018); Iron Quadrangle region (Pezzuti et al. 2021).

Specimens Examined: Brazil, Goiás State, municipalities of Alto Paraíso (ZUFG 1166), São João d'Aliança (ZUFG 1094, ZUFG

Figure 10. Tadpoles of *Adelphobates galactonotus* at Stage 37 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 34(scale 2 mm).

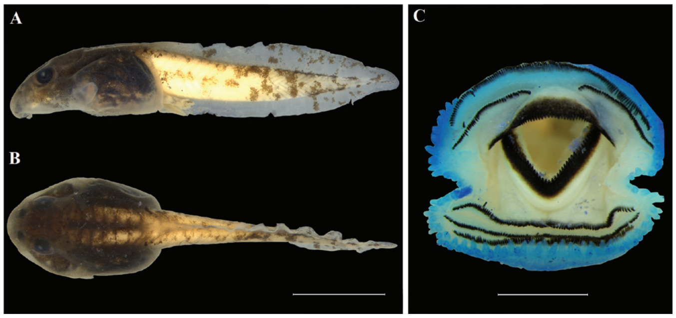

Figure 11. Tadpoles of *Ameerega flavopicta* at Stage 35 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

1110). Description based on four tadpoles between Gosner Stages 35 and 39.

Characterization. Total length 27.06 ± 2.85 mm (Table 1, Figure 11). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.38– 1.49). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of elongated marginal papillae, interrupted by a dorsal gap; few submarginal papillae scattered laterally, of the same length as the marginal papillae. LTRF is 2(2)/3(1), A1<A2, P1<P2>P3. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares medium (ND/ED = 0.18–0.15), elliptical, with a small projection on marginal rim, dorsolaterally positioned. Eyes medium (ED/BH = 0.20–0.24), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.09–0.11) and wide width (SW/BH = 0.15–0.20), opening at the middle third of the body, directed posterodorsally, with the centripetal wall completely fused to the body wall. Vent tube dextral, fused with the ventral fin. The caudal musculature width is medium (TMW/BW = 0.38–0.39). The dorsal fin has medium height (DFH/TMH = 0.59–0.61), originating at the body-tail junction with an acute slope, and convex margin; ventral fin has low to medium height (VFH/TMH = 0.38–0.46) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles analyzed by Dias et al. (2018) closely resemble those described herein. Tadpoles described by Pezzuti et al. (2021) differ by the spiracle length, that they considered short while we considered it medium sized. One individual in our sample presented marginal and submarginal papillae conical in the upper labium.

4. Hylidae Rafinesque 1815

Boana albopunctata (Spix 1824)

First Description of the tadpole: locality not mentioned (De Sá 1995).

Other characterizations: Boracéia – SP, Brazil (Heyer et al. 1990); Nova Itapirema, Engenheiro Schmidt and Vitória Brasil - SP, Brazil (Rossa-Feres & Nomura 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014); Iron Quadrangle region (Pezzuti et al. 2021).

Specimens Examined: Brazil, Goiás State, municipalities of Aparecida do Rio Doce (ZUFG 1812, ZUFG 1822), Cachoeira Alta (ZUFG 1945), Caiapônia (ZUFG 1963), Pirenópolis (ZUFG 07, ZUFG 13), Rio Verde (ZUFG 57). Description based on 15 tadpoles between Gosner Stages 35 and 38.

Characterization. Total length 43.93 ± 8.05 mm (Table 1, Figure 12). The body shape is ovoid in dorsal view and globular-depressed in anterolateral view (BW/BH = 1.09–1.24). The snout is rounded in lateral view. The oral disc is ventral, ventrally emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae absent. LTRF is 2(2)/3(1), A1 = A2; P1 = P2 and P3 with half the length of P2. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower. Nares medium (ND/ED = 0.33–0.34), reniform, with a large projection on the marginal rim, dorsally positioned. Eyes medium (ED/BH = 0.18–0.21), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.12–0.17) and medium width (SW/BH = 0.12–0.12), opening on the posterior third of the body, directed posteriorly, with the centripetal wall not fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.42–0.48). The dorsal fin has medium height (DFH/TMH = 0.62–0.77), originating at the body-tail junction with a median slope, and convex margin; ventral fin is low (VFH/TMHW = 0.40–0.41) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line evident.

Comments. Tadpoles of *B. albopunctata* are found in a diversity of habitats, as temporary streams, swamps, or permanent ponds. Morphological variation of tadpoles related to the environmental changes were described by Rossa-Feres & Nomura (2006). The tadpoles analyzed by Pimenta *et al.* (2014) and Pezzuti et al. (2021) have an oral disc emarginate lateroventral. Tadpoles described by de Sá (1995) differ from our sample by the presence of submarginal papillae and by the teeth row length (P1<P2). The LTRF 2(2)/3(1) observed in our samples also differ from the LTRF observed by Rossa-Feres & Nomura (2006), Pimenta et al. (2014) and Pezzuti et al. (2021), reported as 2(1,2)/3(1).

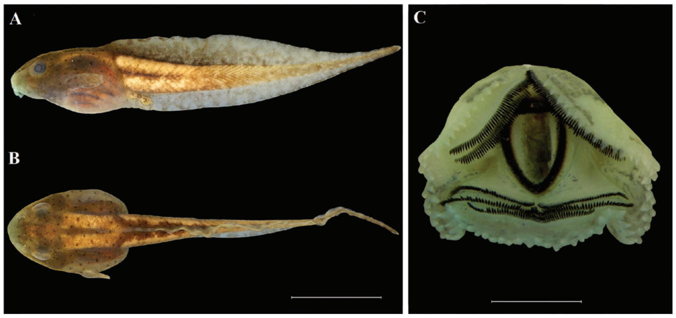

Figure 12. Tadpoles of *Boana albopunctata* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

However, we found the LTRF 2(1,2)/3(1) in our sample, although with a small frequency (2/15), the same of the LTRF 2(2)/3, while the LTRF 2(2)/3(1) was the most common (11/15). In two specimens, the length of the P1 was smaller than the P2, in three, the P1 was longer than the P2, six specimens had the upper jaw sheath M-shaped and in seven tadpoles, the spiracle was posterodorsally directed.

Boana lundii (Burmeister 1856)

First Description of the tadpole: Serra do Cipó – MG, Brazil (Bokermann & Sazima 1973).

Other characterizations: Mirassol – SP, Brazil (Rossa-Feres & Nomura 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014); Iron Quadrangle region (Pezzuti et al. 2021).

Specimens Examined: Brazil, Goiás State, municipality of Iporá (ZUFG 2264, ZUFG 2266). Description based on five tadpoles between Gosner Stages 36 and 38.

Characterization. Total length 59.47 ± 8.98 mm (Table 1, Figure 13). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.08–1.17). The snout is rounded in lateral view. The oral disc is ventral, ventrally emarginate, with a uniseriate row of elongated marginal papillae dorsally, but in alternated disposition only lateroventrally, interrupted by a dorsal gap; submarginal papillae scattered laterally, smaller than the marginal papillae. Accessory teeth row present laterally in the oral disc (*sensu* Sanchez 2010). LTRF is 2(2)/4(1), A1 = A2, P1<P2>P3>P4. The upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares large (ND/ED = 0.38–0.42), reniform, dorsally positioned. Eyes medium (ED/BH = 0.18–0.19), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.09–0.09) and medium width (SW/BH = 0.10–0.14), with opening on the posterior third of the body, directed posterodorsally, with centripetal wall not fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is wide (TMW/BW = 0.52–0.53). The dorsal fin has medium height (DFH/TMH = 0.55–0.61), originating at the body-tail junction with acute slope, and convex margin; ventral fin has low to medium height (VFH/TMH = 0.41–0.50) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line evident.

Comments. Tadpoles described by Bokermann & Sazima (1973) differ analyzed in our study by the ovoid body shape and by the LTRF 2(2)/3(1), although the illustration shows a LTRF 2(2)/4(1), as observed by Rossa-Feres & Nomura (2006). Considering the total length, tadpoles analyzed by Bokermann & Sazima (1973) are larger tadpoles [66 mm, Stage 37), and the described by Rossa-Feres & Nomura (2006) are smaller (45.78 mm, Stages 35–39). Tadpoles described by Rossa-Feres & Nomura (2006) also differ by the row of biseriate marginal papillae (uniseriate in our sample). The tadpoles analyzed by Pimenta et al. (2014) and by Pezzuti et al. (2021) had an oral disc emarginate lateroventrally. Pezzuti et al. (2021) described the spiracle as being short, while we considered it medium sized. Tadpoles of *B. lundii* are easily differentiated from those of *B. albopunctata* by LTRF 2(2)/4(1) (LTRF = 2(2)/3(1), 2(2)/3, or 2(1,2)/3(1) in *B. albopunctata*), marginal rim less prominent, presence of submarginal papillae (absent in *B. albopunctata*), and by the shorter spiracle.

Boana raniceps Cope 1862

First Description of the tadpole: Ibirá – SP, Brazil (Vizotto 1967).

Other characterizations: Argentina (Cei 1980); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Argentina (Kolenc 2008); Bolívia (Schulze et al. 2015).

Specimens Examined: Brazil, Goiás State, municipality of Iporá (ZUFG 879, ZUFG 1028, ZUFG 2256). Description based on 14 tadpoles between Gosner Stages 34 and 38.

Characterization. Total length 57.54 ± 9.54 mm (Table 1, Figure 14). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.07–1.14). The snout is rounded in lateral view. The oral disc is ventral, ventrally emarginate, with a uniseriate row of conical marginal papillae, short, interrupted by a dorsal gap; one to three submarginal papillae scattered laterally, smaller than the marginal papillae. LTRF is 2(1,2)/3(1), A1 = A2, P1<P2>P3. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper and lower jaw sheath had the same width. Nares medium (ND/ED = 0.34–0.37), reniform, with a large projection on the marginal rim, dorsally positioned. Eyes medium (ED/BH = 0.21–0.22), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.07–0.12) and medium width (SW/BH = 0.10–0.13), opening on the posterior third of the body, posterodorsally directed, with centripetal wall not fused to body wall. Vent tube medial with dextral opening, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.47–0.47). The dorsal fin has medium height (DFH/TMH = 0.89–0.94), originating at the body with high slope, and triangular margin; ventral fin has medium height (VFH/TMH = 0.47–0.52) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line evident.

Comments. Tadpoles described by Cei (1980) differ from those studied herein by a dextral vent tube and by the LTRF 2/3 or 2/3(1). Kolenc (2008) reports for tadpoles from Argentina presence of a very short

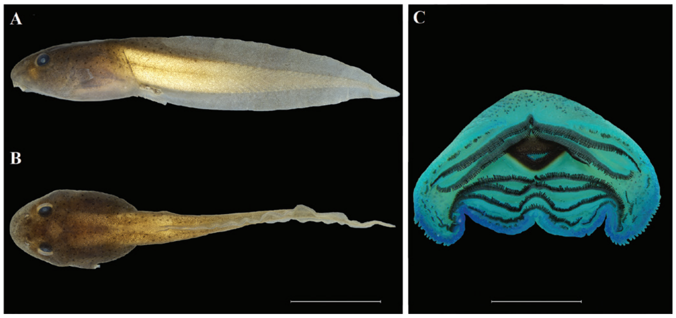

Figure 13. Tadpoles of *Boana lundii* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

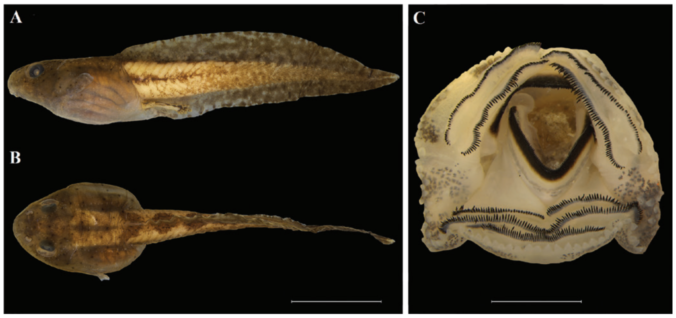

Figure 14. Tadpoles of *Boana raniceps* at Stage 38 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 37 (scale 2 mm).

ventral gap in the marginal papillae, but in one specimen, and a short P4 row in another one. Disregarding these variations, the tadpoles are similar when compared to our sample. The populations analyzed by Schulze et al. (2015) were smaller (total length = 53.4 mm in stages 35 at 41 and our sample = 57.54 in stages 34 at 38). From the total of analyzed individuals, six individuals do not have submarginal papillae, in four, the A2 teeth row was larger than the A1, three have the A1 at the same length of the A2, four have the spiracle posteriorly directed and in two, the lateral line was not evident. *Boana raniceps* tadpoles can be easily distinguished from the tadpoles of *B. albopunctata* and *B. lundii* by the shape of dorsal fin (triangular margin in *B. raniceps*), the LTRF 2(1,2)/3(1) [LTRF 2(2)/3(1) in *B. albopunctata* and 2(2)/4(1) in *B. lundii*], and the presence of conical marginal papillae in *B. raniceps*.

Boana cf. *crepitans*

First Description of the tadpole: not available.

Other characterizations: not available.

Specimens Examined: Brazil, Goiás State, municipality of Nova Roma (ZUFG 2044). Description based on eight tadpoles between Gosner Stages 36 and 39.

Characterization. Total length 62.32 ± 4.96 mm (Table 1, Figure 15). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.13–1.17). The snout is rounded in lateral view. The oral disc is ventral, ventrally emarginate, with a uniseriate row of elongated marginal papillae, in alternated disposition, interrupted by a dorsal gap; few submarginal papillae scattered laterally, smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 = A2, P1 = P2 > P3. The upper jaw sheath is narrow, M-shaped, and the lower jaw sheath is narrow, U-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares are medium (ND/ED = 0.28–0.29), reniform, with a small projection, dorsally positioned. Eyes medium (ED/BH = 0.19–0.20), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.08–0.10) and medium width (SW/BH = 0.11–0.12), opening on the middle third of body, directed posterodorsally, with the centripetal wall fused to the body wall, with distal margin free. Vent tube medial with dextral opening, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.32–0.42). The dorsal fin has medium height (DFH/TMH = 0.59–0.68), originating at the body with median slope, and convex margin; ventral fin is low (VFH/TMH = 0.32–0.40) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line not evident.

Comments. We opt to use the name *Boana* cf. *crepitans* once our tadpoles are notably larger than the available descriptions of *Boana crepitans* tadpoles (53.8 mm of total length for tadpoles from the Iron Quadrangle, Pezzuti et al. 2021; 43.4 mm of total length for tadpole from Serra de São José, Casal & Juncá 2008; 62.3 mm in our study). These tadpoles differ from tadpoles of *B. lundii* by the larger body (BW = 15.24 mm in *B. crepitans* and 11.53 mm in *B. lundii*), ovoid body shape in dorsal view, higher body, wider spiracle, and deeper fins. From the total of analyzed individuals, one does not show submarginal papillae, one individual presented the upper jaw sheath arc-shaped and one the spiracle posteriorly directed, two have accessory teeth rows, and three have the P2 slightly longer than the P1.

Bokermannohyla alvarengai (Bokermann 1956)

First Description of the tadpole: Serra do Cipó – MG, Brazil (Sazima & Bokermann 1977).

Other characterizations: Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014); Iron Quadrangle region (Pezzuti et al. 2021).

Specimens Examined: Brazil, Minas Gerais State, Parque Nacional de Sempre Vivas (ZUFG 974, ZUFG 981). Description based on 15 tadpoles between Gosner Stages 35 and 37.

Characterization. Total length 51.10 ± 5.70 mm (Table 1, Figure 16). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.39– 1.49). The snout is rounded in lateral view. The oral disc is ventral, ventrally emarginate, with a uniseriate row of elongated marginal papillae, interrupted by a dorsal gap; submarginal papillae scattered lateroventrally, smaller than the marginal papillae; accessory teeth rows absent. LTRF is 2(2)/5(1), A1 = A2, P1 < P2 = P3 > P4 > P5. The upper jaw sheath is wide, arc-shaped, and the lower jaw sheath is wide, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares large (ND/ED = 0.42–0.48), elliptical, dorsolaterally positioned. Eyes medium (ED/BH = 0.18–0.20), dorsal positioned. Spiracle sinistral, with medium length (SL/BL = 0.09–0.13) and medium width (SW/BH = 0.15–0.17), opening at the middle third of the body, directed posterodorsally; centripetal wall partially fused to the body wall with a free distal edge. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.32–0.42). The dorsal fin has medium height (DFH/TMH = 0.50–0.56), originating at the body with median slope, and convex margin; ventral fin is low (VFH/TMW = 0.41–0.43) with convex margin; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles described by Sazima & Bokermann (1977) differ from those analyzed herein by having ovoid body shape, and larger total length. In Stage 40, the tadpoles analyzed by Sazima & Bokermann (1977)

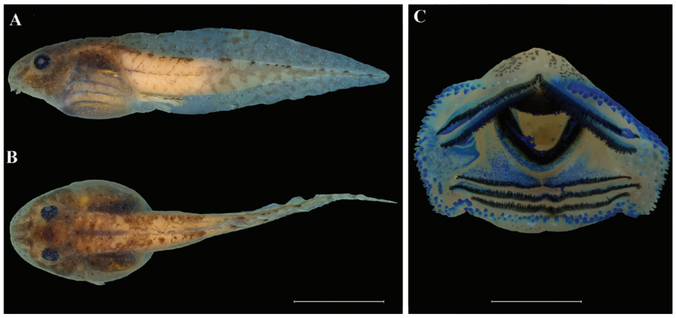

Figure 15. Tadpoles of *Boana* cf. *crepitans* at Stage 39 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

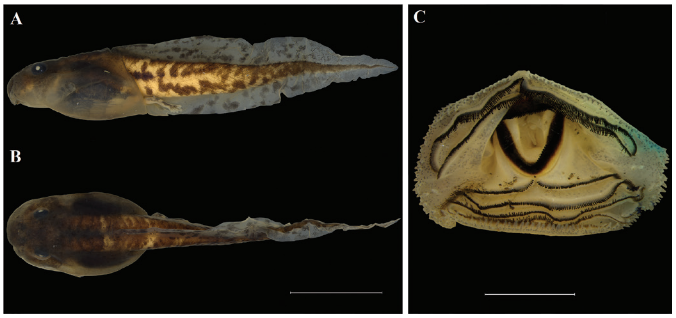

Figure 16. Tadpoles of *Bokermannohyla alvarengai* at Stage 35 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

presented 53 mm, while the tadpoles in our sample, Stages 35–39, had about 51.10 mm. Tadpoles described by Pezzuti et al. (2021) also were larger (56.1 mm) than the tadpoles that we described, and had medium sized nares, while we considered it larger. The oral disc of the tadpoles from the Iron Quadrangle also had lateroventrally emargination and marginal papillae with alternate disposition (Pezzuti et al. 2021). Although the illustration presented by Sazima & Bokermann (1977) show the LTRF 2(1,2)/5(1), the authors describe it as 2(2)/5(1), the same observed by Pimenta et al. (2014) and in our sample.

Bokermannohyla pseudopseudis (Miranda-Ribeiro 1937)
First Description of the tadpole: Alto Paraíso de Goias – GO, Brazil (Lins et al. 2018).
Other characterizations: Not available.
Specimens Examined: Brazil, Goiás State, municipality of Cavalcante (ZUFG 2426, ZUFG 2427). Description based on ten tadpoles between Gosner Stages 31 and 37.
Characterization. Total length 42.95 ± 4.32 mm (Table 1, Figure 17). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.05–1.12). The snout is rounded in lateral view. The oral disc is ventral, emarginate ventrally, with a uniseriate row of elongated marginal papillae, in alternated disposition, interrupted by a dorsal gap; submarginal papillae scattered laterally, smaller than the marginal papillae, accessory teeth rows present laterally in the oral disc. LTRF is 3(1,3)/6(1), A1 slightly smaller than A2 and A3 slightly smaller than A2; P1 = P2 = P3 = P4 = P5 > P6. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is wide, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares large (ND/ED = 0.38–0.40), elliptical, with a small projection on the marginal rim, dorsally positioned. Eyes medium (ED/BH = 0.18–0.20), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.10–0.13) and medium width (SW/BH = 0.14–0.15), opening at the middle third of the body, directed posterodorsally, with the centripetal wall fused to the body wall, with a free distal edge. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium to wide (TMW/BW = 0.47– 0.55). The dorsal fin has medium height (DFH/TMH = 0.67–0.70), originating at the body with a median slope, and convex margin; ventral fin has medium height (VFH/TMHW = 0.47–0.48) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral lines evident.
Comments. A previous description of *B. pseudopseudis* tadpoles was provided by Eterovick & Brandão (2001) but was based on a mixed series of both *B. pseudopseudis* and *B. sapiranga* tadpoles (Brandão et al. 2012; Lins et al. 2018). Thus, we considered the first formal description of the tadpole the report by Lins et al. (2018), once only *B. pseudopseudis* tadpoles were used in the characterization. The tadpole described by Lins et al. (2018) were larger (TL = 65.04 mm in stage 25) than those described herein (TL = 42.95 mm) and had a different LTRF: 3(1, 2)/6(1). From the total of analyzed individuals, two presented fewer submarginal papillae scattered laterally in the oral disc; two individuals presented a small ventral gap in the marginal papillae, with the space of one papilla; and three individuals presented LTRF 2(2)/6(1). Accessory tooth rows are "*short tooth rows in the lateral areas of the oral disc and beside the jaw sheaths*" (Sánchez 2010) and was reported frequently for tadpoles with high number of tooth rows [at least 2/4, *Boana balzani* and *B. palaestes* (Duellman *et al.* 1997), *B. riojana* (Kolenc *et al.* 2008), *Hyloscirtus* tadpoles (Sánchez, 2010), *Bokermannohyla pseudopseudis* group (Eterovick and Brandão, 2001; Faivovich *et al.* 2005), *Trachycephalus typhonius*, Nomura per. obs.], but was already observed for tadpoles with fewer tooth rows [no more than 2/3, *B. cordobae* (Kolenc *et al.* 2008)].

Bokermannohyla sapiranga Brandão, Magalhães, Garda, Campos, Sebben & Maciel 2012
First Description of the tadpole: Brasília– DF, Brazil (Lins et al. 2018).
Other characterization: Not available.
Specimens Examined: Brazil, Goiás State, municipality of Pirenópolis (ZUFG 217, ZUFG 218, ZUFG 2430). Description based on five tadpoles between Gosner Stages 25 and 28.
Characterization. Total length 59.51 ± 15.30 mm (Table 1, Figure 18). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.14–1.19). The snout is rounded in lateral view. The oral disc is ventral, emarginate ventrally, with a uniseriate row of elongated marginal papillae, biseriate laterally, interrupted by a dorsal gap; submarginal papillae scattered laterally, smaller than the marginal papillae; accessory teeth row present laterally in the oral disc. LTRF is 2(2)/5(1), A1 = A2; P1 = P2 = P3 = P4 > P5. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, V- shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares medium to large (ND/ED = 0.35–0.43), elliptical, with a projection on marginal rim, dorsally positioned. Eyes small (ED/BH = 0.14–0.18), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.09–0.10) and medium width (SW/BH = 0.14–0.17), opening at the middle third of the body, directed posterodorsally, with the centripetal wall fused to the body wall and with a free distal edge. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium to wide

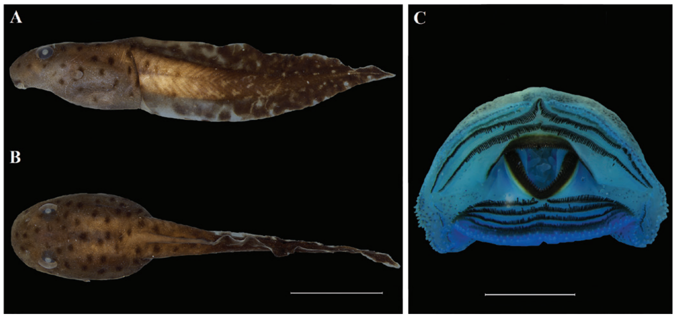

Figure 17. Tadpoles of *Bokermannohyla pseudopseudis* at Stage 25 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

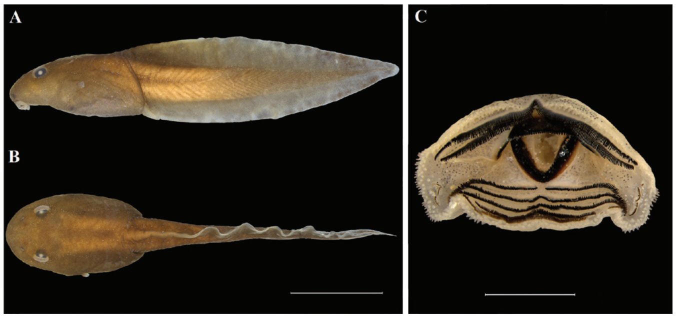

Figure 18. Tadpoles of *Bokermannohyla sapiranga* at Stage 25 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

(TMW/BW = 0.45–0.69). The dorsal fin has low to medium height (DFH/TMH = 0.41–0.64), originating at the body with an acute slope, and margin convex to the caudal musculature; ventral fin has low to medium height (DFH/TMH = 0.30–0.53) with parallel margin; the tail tip is pointed. Lateral line evident.

Comments. From the total of analyzed individuals, four presented alternated marginal papillae, three had accessory teeth rows laterally, one presented marginal papilla in the upper labium, and three presented P1<P2. Tadpoles analyzed by Lins et al. (2018) closely resemble those presented herein, with the exception that the accessory teeth rows were absent in their populations and described as a variation presented in only one individual. Tadpoles of *B. sapiranga* can be distinguished of the *B. alvarengai* and *B. pseudopseudis* by the larger total length: *Bokermannohyla alvarengai* = 51.10 mm, Stages 35–37; *B. pseudopseudis* = 42.95 mm, Stages 31–37; *B. sapiranga* = 59.51 mm, Stages 25–28. Also, tadpoles of *B. sapiranga* differ from *B. alvarengai* larvae by the uniseriate marginal papillae laterally and from *B. pseudopseudis* by the LTRF. The presence of accessory teeth rows laterally in the oral disc was observed only in *B. pseudopseudis* and in *B. sapiranga*, and this trait is considered a synapomorphy for the *B. pseudopseudis* group [Eterovick & Brandão 2001; Faivovich et al. 2005; however, see a discussion in Sánchez (2010) for the phylogenetic importance of this trait].

Dendropsophus minutus (Peters 1872)

First Description of the tadpole: Campo Grande – SP, Brazil (Bokermann 1963). Wrongly attributed to the municipality of Campo Grande in the state of Mato Grosso do Sul, Brazil, by Rossa-Feres & Nomura (2006). Other characterizations: Northwestern Region of São Paulo State, Brazil (Vizotto 1967); Trinidad and Tobago (Kenny 1969); Santa Cecília – Ecuador (Duellman 1978); Argentina (Cei 1980); Boracéia – SP, Brazil (Heyer et al. 1990); Venezuela (Duellman 1997); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014); Bolivia (Schulze et al. 2015); Iron Quadrangle region (Pezzuti et al. 2021). Although lacking a formal characterization, some larval traits can be found in available taxonomic keys for the tadpoles from the Amazonas (Hero 1990) and Colombia (Lynch & Mayorga 2011).

Specimens Examined: Brazil, Goiás State, municipalities of Aruanã (ZUFG 610), Bonfinópolis (ZUFG 1952), Jataí (ZUFG 714), Pirenópolis (ZUFG 196), Portelândia (ZUFG 738), Serranópolis (ZUFG 216), and Minas Gerais State, municipality of Campina Verde (ZUFG 1953). Description based on 15 tadpoles between Gosner Stages 34 and 39.

Characterization. Total length 34.63 ± 5.17 mm (Table 1, Figure 19). The body shape is elliptical elongated in dorsal view and triangular-compressed in lateral view (BW/BH = 0.86–0.95). The snout is rounded in lateral view. The oral disc anteroventral, not emarginate, with a uniseriate row of elongated marginal papillae, biseriate ventrally, interrupted by a dorsal gap; submarginal papillae absent. LTRF varies among 0/0, 0/1, 0/2, 1/1 and 1/2. The upper jaw sheath is wide, arc-shaped, and the lower jaw sheath is wide, U-shaped; the upper jaw sheath is slightly wider than the lower. Nares medium (ND/ED = 0.20–0.22), rounded, laterally positioned. Eyes large (ED/BH = 0.30–0.33), laterally positioned. Spiracle sinistral, short (SL/BL = 0.02–0.04), narrow (SW/BH = 0.05–0.07), with opening at the middle third of the body, directed posteriorly, with the centripetal wall completely fused to the body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is wide (TMW/BW = 0.58–0.59), with the anterior third of the tail muscle and adjacent fins with a sheath of thick connective tissue. The dorsal fin has medium height (DFH/TMH = 0.80–0.91), originating at the posterior third of the body with a median slope, and triangular margin; ventral fin is high (VFH/TMH = 1.15–1.15) with a triangular margin; the tail tip ends in a flagellum. Lateral line not evident.

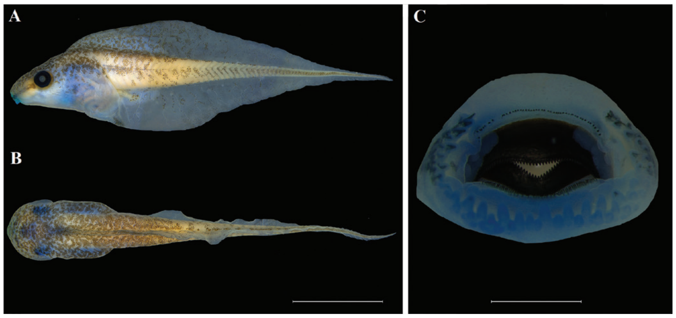

Figure 19. Tadpoles of *Dendropsophus minutus* at Stage 37 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

Comments. Variations in some morphological characteristics, as body shape [cited as ovoid by Vizotto (1967) and Duellman (1978), and elliptical by Heyer (1990) and Rossa-Feres & Nomura (2006)] and eyes position [cited as dorsolaterally by Heyer (1990)], represent a terminology difference among the descriptions. Our sampled populations are like those described from Campo Grande (Bokermann 1963), but are smaller, with marginal papillae uniseriate laterally, have a different labial teeth row formula and spiracle directed posteriorly. However, the total length of the tadpoles of *D. minutus* is highly variable throughout its distribution [our sample = 34.63 mm, Stages 34–39; Iron Quadrangle = 35.4, stage 30 (Pezzuti et al. 2021); Northwestern Region of São Paulo State = 36.5 mm, Stage 36 (Vizotto 1967); Nova Itapirema and Macaúbas = 37.52 mm, Stages 37–40 (Rossa-Feres & Nomura 2006); San Sebastián = 37.60 mm, Stages 36–41 (Schulze et al. 2015); Campo Grande = 30 mm, probably Stage 39 (Bokermann 1963); Trinidad and Tobago = 40 mm, Stages 31–39 (Kenny 1965); Ecuador = 41.7 mm, Stage 41 (Duellman 1978); Venezuela = 39.35, Stage 37 (Duellman 1997) and Los Lagos = 36.9 mm, Stages 37 (Schulze et al. 2015)]. In relation to marginal papillae, the tadpoles analyzed in this study resemble those described by Rossa-Feres & Nomura (2006), presenting marginal papillae row uniseriate laterally and biseriate ventrally, but differ in the shape of papillae, which was considered long and triangular by the authors. However, this trait was also highly variable. The marginal papillae of *D. minutus* could be biseriate ventrally and uniseriate laterally (Bokermann 1963, although the illustration show a biseriate papillae also laterally; Vizotto 1967, Rossa-Feres & Nomura 2006, our sample), biseriate ventrally and in alternate disposition laterally (*D. minutus* A, Schulze et al. 2015); biseriate ventrally and laterally (Duellman 1978, Heyer 1990); or uniseriate ventrally and laterally (Kenny 1969; *D. minutus* B, Schulze et al. 2015; Pezzuti et al. 2021, but with alternate disposition). Despite the LTRF 0/1 was the most common in this study, observed in six of the 15 individuals [variation also registered by Rossa-Feres & Nomura (2006) and Pimenta et al. (2014)], this trait varied among 0/0 [two individuals, variation also registered by Rossa-Feres & Nomura (2006)], 0/2 [three individuals, variation also registered by Duellman, (1978)], 1/2 [three individuals, variation also registered by Vizotto (1967), Cei (1980), Heyer (1990), Rossa-Feres & Nomura (2006), and Pezzuti et al. (2021)], and 1/1 (one individual, registered for the first time). When the P2 is present, it is much smaller than P1 (Vizotto 1967, Heyer 1990, Schulze et al. 2015, Pezzuti et al. 2021, our sample), being the P1 = P2 a rare state (Rossa-Feres & Nomura 2006). In our sample, ten tadpoles presented the spiracle posteriorly directed, similar to those observed in the illustration presented by Bokermann (1967) and Kenny (1969), and description provided by Heyer (1990), but three tadpoles had the spiracle directed porsterodorsally, as the descriptions presented by Vizotto (1967), by Duellman (1978), by Rossa-Feres & Nomura (2006), by Schulze et al. (2015), and Pezzuti et al. (2021). From the total of analyzed individuals, seven presented nares elliptical. Gehara et al. (2014) defined *D. minutus* as a species complex, as noted by Duellman (1997). We do not test this hypothesis using tadpoles' traits, but we did not find any association between the observed variations and the divergent evolutionary lineage proposed by Gehara et al. (2014).

Dendropsophus soaresi (Caramaschi & Jim 1983)
First Description of the tadpole: Jandaíra – BA, Brazil (Gomes & Peixoto 1991).
Other characterization: Not available.
Specimens Examined: Brazil, Goiás State, municipalities of Barro Alto (ZUFG 811, ZUFG 862) and Jataí (ZUFG 773). Description based on ten tadpoles between Gosner Stages 35 and 39.
Characterization. Total length 36.88 ± 1.93 mm (Table 1, Figure 20). The body shape is elliptical elongated in dorsal view and triangular-compressed in lateral view (BW/BH = 1.07–1.07). The snout is sloped in lateral view. The oral disc anteroventral, not emarginate, with a biseriate row of rounded marginal papillae (varying between four to eight marginal papillae laterally), interrupted by a dorsal and lateroventral gap; submarginal papillae absent. LTRF is 0/1, with the P1 teeth row located close to the lower jaw sheath. The upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is wide, U-shaped; the lower jaw sheath is wider than the upper jaw sheath. Nares medium (ND/ED = 0.17–0.20), rounded, anteriorly positioned. Eyes large (ED/BH = 0.29–0.31), laterally positioned. Spiracle sinistral, short (SL/BL = 0.04–0.05), with medium width (SW/BH = 0.09–0.11), opening at the middle third of the body, directed posteriorly, with centripetal wall completely fused to the body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is wide (TMW/BW = 0.57–0.58). The dorsal fin has medium height (DFH/TMH = 0.58–0.78), originating on the posterior third of the body with a median slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.59–0.80) and with convex margin; the tail tip end in a flagellum. Lateral line not evident.
Comments. Our sample of *D. soaresi* tadpoles closely resemble those described by Gomes & Peixoto (1991) but are larger [our sample = 36.88 mm of total length, Stages 35–38; Jandaíra = 29.5 mm, Stages 34–38, (Gomes & Peixoto 1991). The population described from Jandaíra, also have longer marginal papillae. From the ten individuals observed in our sample, three presented elliptical nares, and one had a small projection on the nares marginal rim. The spiracle direction also varied, with one specimen presenting spiracle ventrally directed and three posterodorsally directed. Tadpoles of *D. minutus* are commonly mistaken by tadpoles of *D. soaresi*, but tadpoles of *D. soaresi* can be identified by the presence of lateroventral gaps in the row of marginal papillae, the lower jaw sheath wider and straighter than in *D. minutus,* and the absence of blackish band between the snout and eyes, common in *D. minutus.*

Scinax fuscomarginatus (Lutz 1925)
First Description of the tadpole: Nova Itapirema – SP, Brazil (Vizotto 1967).
Other characterizations: Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014).
Specimens Examined: Brazil, Goiás State, municipality of Niquelândia (ZUFG 915). Description based on ten tadpoles between Gosner Stages 34 and 39.
Characterization. Total length 30.72 ± 1.68 mm (Table 1, Figure 21). The body shape is elliptical in dorsal view and triangular-depressed in lateral view (BW/BH = 1.09–1.17). The snout is rounded in lateral view. The oral disc is ventral, folded ventrally, with a uniseriate row of elongated marginal papillae, in alternated disposition only laterally, interrupted by a dorsal gap; submarginal papillae aggregate laterally, smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 = A2, P1 = P2 = P3. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the lower jaw sheath is slightly wider than the upper jaw sheath. Nares medium (ND/ED = 0.28–0.28), rounded, dorsally positioned. Eyes large (ED/BH = 0.29–0.30), laterally positioned. Spiracle sinistral, with medium length (SL/BL = 0.14–0.18) and medium to wide width (SW/BH = 0.20–0.26), opening on the posterior third of the body, posterodorsally directed, with the centripetal wall fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium to wide (TMW/BW = 0.47–0.51).

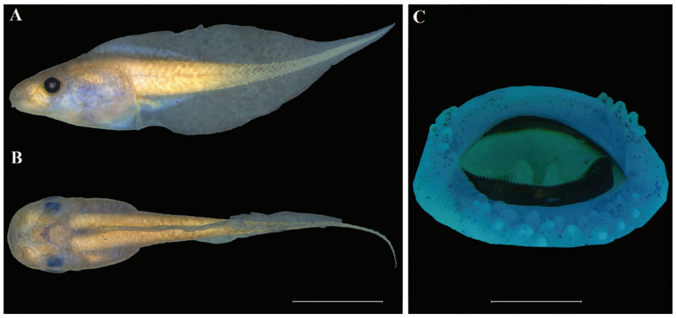

Figure 20. Tadpoles of *Dendropsophus soaresi* at Stage 37 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

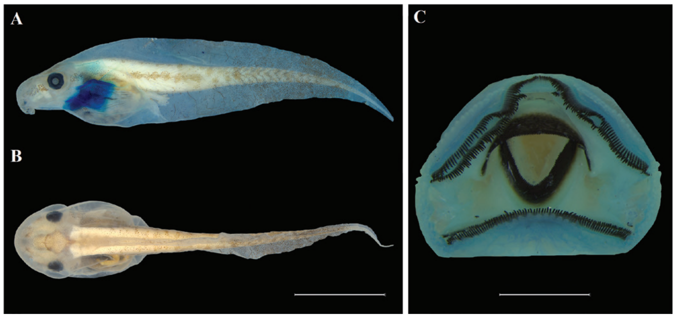

Figure 21. Tadpoles of *Scinax fuscomarginatus* at Stage 35 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

The dorsal fin has medium height (DFH/TMH = 0.86–0.94), originating at the body with median slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.76–0.77) with a convex margin; the tail tip end in a flagellum. Lateral line not evident.

Comments. Tadpoles described by Vizotto (1967) differ from our sample by the LTRF 2(2)/3, however the author reports that the LTRF 2(2)/3(1) was also observed. Tadpoles described by Vizotto (1967) also have the P1 teeth row with the same length of the P2 and the P3 with about half the length of P1 and P2. Tadpoles described by Rossa-Feres & Nomura (2006) have the P1 teeth row smaller than the P2 and the P3 (P1>P2>P3 in our sample). From the total of analyzed individuals, one had fewer number of submarginal papillae that formed a row on the sides of the oral disc, one individual has the A1 teeth row with the same length than the A2 and one the upper jaw sheath M-shaped.

Scinax fuscovarius (Lutz 1925)

First Description of the tadpole: Northwestern region of São Paulo State, Brazil (Vizotto 1967).

Other characterizations: Argentina (Cei 1980, Fabrezi & Vera 1997); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014); Bolívia (Schulze et al. 2015).

Specimens Examined: Brazil, Goiás State, municipalities of Iporá (ZUFG 2091, ZUFG 2099, ZUFG 2103), Niquelândia (ZUFG 2061), Silvânia (ZUFG 1274) and Parque Nacional das Emas (ZUFG 1317). Description based on ten tadpoles between Gosner Stages 34 and 39.

Characterization. Total length 42.14 ± 3.76 mm (Table 1, Figure 22). The body shape is elliptical in dorsal view and triangular-compressed in lateral view (BW/BH = 0.88–0.89). The snout is sloped in lateral view. The oral disc is anteroventral, folded ventrally, with a uniseriate row of elongated marginal papillae, interrupted by a dorsal gap; submarginal papillae at commissures, smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 = A2, P1 = P2 > P3. The upper jaw sheath is wide, arc-shaped, and the lower jaw sheath is wide, U-shaped; the upper jaw sheath is slightly wider than the lower jaw sheath. Nares medium (ND/ED = 0.27–0.30), rounded, dorsolaterally positioned. Eye medium (ED/BH = 0.25–0.25), laterally positioned. Spiracle sinistral, with medium length (SL/BL = 0.15–0.16) and medium width (SW/BH = 0.09–0.18), opening on the posterior third of the body, posterodorsally directed, with the centripetal wall fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is wide (TMW/BW = 0.52–0.57). The dorsal fin has medium height (DFH/TMH = 0.84–0.87), originating at the body with high slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.63–0.92) with convex margin; the tail end with a flagellum. Lateral line evident.

Comments. Our tadpoles are like those described by Vizotto (1967) and Cei (1980), differing only by the disposition of submarginal papillae, with 4 to 6 rows laterally in the oral disc in these tadpoles. Tadpoles described by Rossa-Feres & Nomura (2006) differ from our samples by the upper jaw sheath M-shaped and nares elliptical. The populations described by Schulze et al. (2015) had the upper jaw-sheath M-shaped, oral disc emarginated laterally and were smaller (total length = 32.32 mm, Stages 32–38) than our tadpoles (TL = 42.13 mm, Stages 35–39). One individual in our sample presented the upper jaw sheath M-shaped and the spiracle posteriorly directed. Tadpoles of *S. fuscovarius* can be distinguished of those of *S. fuscomarginatus* by the sloped snout shape in lateral view (rounded in *S. fuscomarginatus*), deeper body and higher fins.

Scinax longilineus (Lutz 1968)

First Description of the tadpole: Poços de Caldas – MG, Brazil (Andrade & Cardoso 1991).

Other characterizations: not available.

Specimens Examined: Brazil, Minas Gerais State: Poços de Caldas (ZUFG 2494, ZUFG 2495, ZUFG 2496). Description based on 11 tadpoles between Gosner Stages 35 and 40.

Characterization. Total length 38.49 ± 4.91 mm (Table 1, Figure 23). The body shape is rounded in dorsal view and globular-depressed in lateral view (BW/BH = 0.95–1.00). The snout is rounded in lateral view. The oral disc is anteroventral, not emarginate, with a uniseriate row of conical marginal papillae, in alternated disposition, biseriate laterally, interrupted by a dorsal gap; submarginal papillae aggregated laterally, smaller than the marginal papillae. LTRF is 2(2)/3, A1 = A2, P1 = P2 = P3. The upper jaw sheath is narrow, M-shaped, and the lower jaw sheath is narrow, U-shaped; the upper jaw sheath is slightly wider than the lower jaw sheath. Nares medium (ND/ED = 0.20–0.24), rounded, dorsally positioned. Eyes small to medium (ED/BH = 0.15–0.20), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.07–0.12) and medium width (SW/BH = 0.10–0.12), opening on the posterior third of the body, posterodorsally directed, with centripetal wall fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium to wide (TMW/BW = 0.45–0.49). The dorsal fin has medium height (DFH/TMH = 0.72–0.73), originating at the body with acute slope, and convex margin; ventral fin has medium height (VFH/TMW = 0.54–0.60) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line evident.

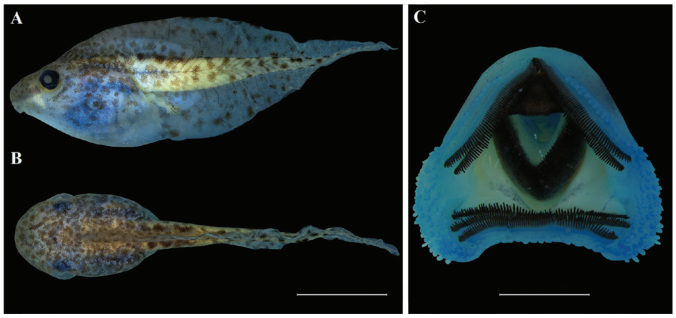

Figure 22. Tadpoles of *Scinax fuscovarius* at Stage 38 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

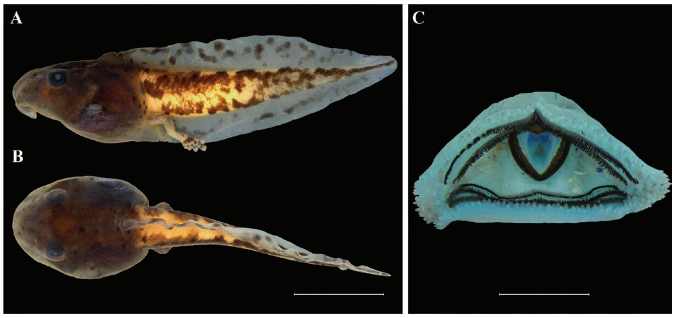

Figure 23. Tadpoles of *Scinax longilineus* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

Comments. Tadpoles analyzed in this study were collected in the type locality of the species and differ from the original description by the body rounded in dorsal view, and nares dorsally positioned (body elliptical and nares dorsolaterally positioned in Andrade & Cardoso 1991). From the 11 analyzed individuals in our sample, one presented body elliptical and the A1 teeth row longer than the A2. Tadpoles of *S. longilineus* have an oral disc with a concave posterior margin when closed, a shared trait for tadpoles in the *S. catharinae* group, differing from the other species of *Scinax*. This trait allows an easy differentiation of *S. longilineus* tadpoles from *S. fuscomarginatus*, and *S. fuscovarius* tadpoles.

Scinax pombali Lourenço, Carvalho, Baêta, Pezzuti & Leite 2013
First Description of the tadpole: Capitólio – MG, Brazil (Lourenço et al. 2013).
Other characterization: Not available.
Specimens Examined: Brazil, Minas Gerais State, Parque Nacional da Serra da Canastra (ZUFG 2493, 2899). Description based on ten tadpoles between Gosner Stages 36 and 40.
Characterization. Total length 46.07 ± 3.19 mm (Table 1, Figure 24). The body shape is rounded in dorsal view and globular-depressed in lateral view (BW/BH = 1.12–1.17). The snout is rounded in lateral view. The oral disc is ventral, folded ventrally and ventrolaterally, with a biseriate row of mixed conical and elongated marginal papillae, without dorsal gap; presence of submarginal papillae aggregated lateroventrally, mixing small and large submarginal papillae, also mixing submarginal papillae that were smaller and larger than marginal papillae; submarginal papillae when larger than marginal papillae could have lateral projection, forming a T-shape. LTRF is 2(2)/3, A1 = A2, P1 = P2 = P3. The upper jaw sheath is narrow to medium sized, M-shaped, the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares medium (ND/ED = 0.16–0.23), rounded, dorsally positioned. Eyes medium (ED/BH = 0.22–0.23), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.08–0.09), narrow width (SW/BH = 0.08–0.09), with opening on the posterior third of the body, posterodorsally directed, with centripetal wall not fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is wide (TMW/BW = 0.55–0.56). The dorsal fin has low to medium height (DFH/TMH = 0.37–0.55), originating at the body with a median slope, and convex margin; ventral fin low (VFH/TMW = 0.28–0.40) with convex margin; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles described by Lourenço et al. (2013) present snout sloped or truncated in lateral view (rounded in our samples). The large oral disc, continuous row of marginal papillae, without a dorsal gap, and the amount and shape of the submarginal papillae are useful traits that help to distinguish the tadpoles of *Scinax pombali* from the tadpoles of other species of *Scinax* included in our study. In our sample, one individual presented the marginal papillae uniseriate in alternate disposition and biseriate laterally, and another individual had A2 slightly smaller than A1.

Scinax rupestris Araújo-Vieira, Brandão & Faria 2015
First Description of the tadpole: Chapada dos Veadeiros National Park – GO, Brazil (Araujo-Vieira et al. 2015).
Other characterization: not available.
Specimens Examined: Brazil, Goiás State, Parque Nacional da Chapada dos Veadeiros (ZUFG 1970, ZUFG 2243, ZUFG 2251, ZUFG 2276). Description based on 11 tadpoles between Gosner Stages 31 and 37.
Characterization. Total length 32.04 ± 3.59 mm (Table 1, Figure 25). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.01–1.06). The snout is rounded in lateral view. The oral disc is anteroventral, not emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae aggregated laterally, and smaller than the marginal papillae. LTRF is 2(2)/3 or 2(2)/3(1), A1 = A2, P1 = P2 and P3 slightly smaller than P1 and P2; the upper jaw sheath is wide, M-shaped, and the lower jaw sheath is wide, V-shaped; the upper jaw sheath is wider than the lower. Nares small to medium (ND/ED = 0.08–0.15) rounded, dorsally positioned. Eyes medium (ED/BH = 0.23–0.24), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.08–0.12) and medium width (SW/BH = 0.13–0.17), opening at the middle third of the body, posterodorsally directed, with centripetal wall fused to the body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.32–0.37). The dorsal fin has medium height (DFH/TMH = 0.54–0.83), originating at the body with median slope, and convex margin; ventral fin has medium height (VFH/TMW = 0.52–0.54) with convex margin; the tail tip is pointed. Lateral line not evident.
Comments. Tadpoles analyzed in this study closely resemble those described by Araujo-Vieira et al. (2015), differing only by the length of teeth rows and the shape of the upper jaw sheath (A1 > A2, P1 = P2 = P3, and upper jaw arc-shaped), although the figure of the oral disc in the original description shows an M-shaped upper jaw sheath. *Scinax rupestris* tadpoles can be distinguished from the tadpoles of

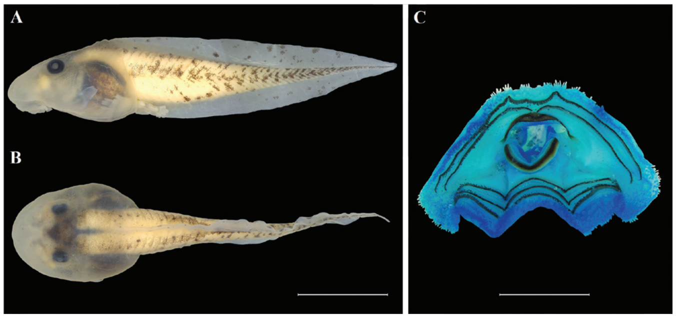

Figure 24. Tadpoles of *Scinax pombali* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

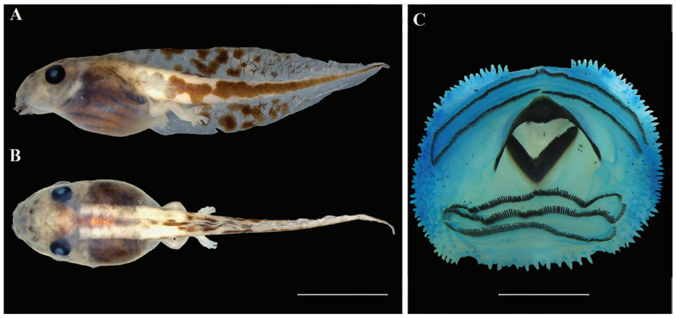

Figure 25. Tadpoles of *Scinax rupestris* at Stage 40 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 30 (scale 2 mm).

S. fuscomarginatus and *S. fuscovarius* by oral disc not emarginated (oral disc ventrally emarginated in *S. fuscomarginatus* and *S. fuscovarius*), and upper jaw sheath in M-shaped differ of *S. fuscomarginatus* (arc-shaped). The body shape elliptical in dorsal view and oral disc without a concave posterior differ *S. rupestris* of *S. longilineus* (body shape rounded and oral disc with a concave posterior margin when closed). The LTRF 2(2)/3(1), the most common in our sample, is described as a variation in the original description (Araujo-Vieira et al. 2015). We also observed a variation in the density of pigmentation in the body coloration, as reported by Araujo-Vieira *et al.* (2015). Two individuals from our sample had the body ovoid in dorsal view, two showed an evident lateral line, two had the LTRF 2(2)/3, three had fewer submarginal papillae, scattered lateroventrally, and three had the A1 teeth row of the same length than the A2.

Scinax similis (Cochran 1952)
First Description of the tadpole: Rio de Janeiro – RJ, Brazil (Alves & Carvalho-e-Silva 1999).
Other characterizations: Not available.
Specimens Examined: Brazil, Goiás State, municipalities of Mineiros (ZUFG 70), Niquelândia (ZUFG 645) and Parque Nacional da Chapada dos Veadeiros (ZUFG 2124). Description based on ten tadpoles between Gosner Stages 31 and 37.

Characterization. Total length 30.12 ± 2.01 mm (Table 1, Figure 26). The body shape is elliptical in dorsal view and triangular-compressed in lateral view (BW/BH = 0.90–0.94). The snout is rounded in lateral view. The oral disc is anteroventral, ventrally emarginate, with a uniseriate row of conical marginal papillae, in alternate disposition, interrupted by a dorsal gap; submarginal papillae aggregate laterally, of the same size as the marginal papillae. LTRF is 2(2)/3(1), A1 = A2, P1 > P2 > P3. The upper jaw sheath is narrow, M-shaped, and the lower jaw sheath is narrow, V-shaped; the lower jaw sheath is slightly wider than the upper jaw sheath. Nares medium (ND/ED = 0.21–0.33), rounded, dorsolaterally positioned. Eyes large (ED/BH = 0.29–0.31), laterally positioned. Spiracle sinistral, medium to long (SL/BL = 0.12–0.21), with medium width (SW/BH = 0.14–0.17), opening on the posterior third of the body, posterodorsally directed, with centripetal wall fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is wide (TMW/BW = 0.51–0.55). The dorsal fin has medium height (DFH/TMHW = 0.85–0.87), originating at the body with acute slope, and convex margin; ventral fin has medium height (VFH/TMW = 0.67–0.74) with convex margin; the tail end with a flagellum. Lateral line evident.

Comments. Tadpoles described by Alves & Carvalho-e-Silva (1999) had arc-shaped upper jaw sheath and fewer submarginal papillae scattered laterally. Otherwise, our sample closely resemble those tadpoles. In our sample, two individuals had the upper jaw sheath arc-shaped, which indicates that this variation would be common within and among *S. similis* population. Tadpoles of *S. similis* are smaller and the dorsal fin origin is closer to the eyes than in *S. fuscovarius*. Tadpoles of *S. similis* can also be distinguished from *S. fuscovarius* by the snout rounded, narrower jaw sheath and smaller total length. Also, *S. similis* can be distinguished from *S. fuscomarginatus* by the wider lower jaw sheath and the P3 teeth row being slightly smaller than the P1 and P2 teeth rows. Easily distinguished from *S. rupestris* due to the oral disc ventrally emarginated.

Scinax gr. *ruber*
First Description of the tadpole: Species uncertain.
Other characterizations: Not available.
Specimens Examined: Brazil, Goiás State, municipality of Nova Roma (ZUFG: 1881). Description based on four tadpoles between Gosner Stages 31 and 40.

Total length 29.92 ± 3.35 mm (Table 1, Figure 27). The body shape is ovoid in dorsal view and triangular-compressed in lateral view (BW/BH = 0.84–0.96). The snout is sloped in lateral view. The oral disc is anteroventral, ventrally emarginate, with a uniseriate row of elongate marginal papillae, in alternate disposition, interrupted by a dorsal gap; submarginal papillae aggregate laterally, smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 = A2, P1 = P2 > P3. The upper jaw sheath is narrow, M-shaped, and the lower jaw sheath is narrow, V-shaped; the lower jaw sheath is slightly wider than the upper jaw sheath. Nares medium (ND/ED = 0.20–0.25), rounded, laterally positioned. Eyes medium (ED/BH = 0.26–0.27), laterally positioned. Spiracle sinistral, with medium length (SL/BL = 0.12–0.15) and medium width (SW/BH = 0.13–0.15), opening on the middle third of the body, posterodorsally directed, with centripetal wall fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.41–0.45). The dorsal fin has medium height (DFH/TMH = 0.93–0.97), originating at the body with median slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.68–0.74) with convex margin; the tail tip the tail end with a flagellum is pointed. Lateral line not evident.

Comments. We were unable to associate these tadpoles to *S. fuscovarius*, once these tadpoles are smaller and had smaller fins, to *Scinax similis*,

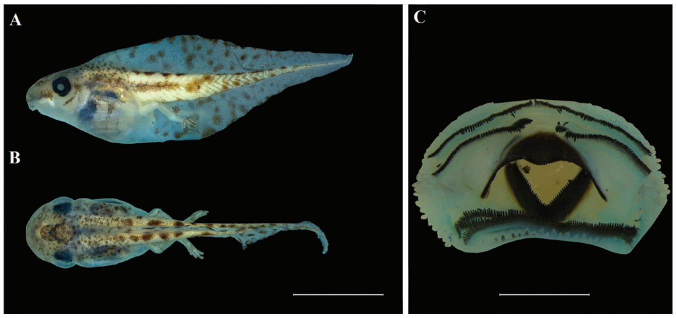

Figure 26. Tadpoles of *Scinax similis* at Stage 39 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

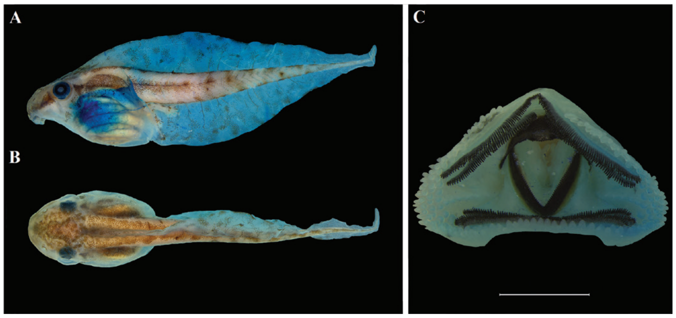

Figure 27. Tadpoles of *Scinax* gr. *ruber* at Stage 37 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

due to the snout sloped in lateral view, nares with opening laterally directed (anterolaterally directed in *S. similis*), and to *S. fuscomarginatus* due to the position of fin origin, away from the eyes position, and deeper fins. They also are distinguished from *S. rupestris* by the oral disc ventrally emarginated.

Scinax squalirostris (Lutz 1925)

First Description of the tadpole: Paranapiacaba – SP, Brazil (Bokermann 1967).

Other characterizations: Jaboticatubas – MG, Brazil (Cei 1980), Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014).

Specimens Examined: Brazil, Minas Gerais State, Parque Nacional da Serra da Canastra (ZUFG 2497, ZUFG 2498). Description based on six tadpoles between Gosner Stages 31 and 36.

Characterization. Total length 22.58 ± 1.05 mm (Table 1, Figure 28). The body shape is elliptical in dorsal view and triangular-compressed in lateral view (BW/BH = 0.96–1.08). The snout is rounded in lateral view. The oral disc is anteroventral, ventrally emarginate, with a uniseriate row of conical marginal papillae, interrupted by dorsal gap; submarginal papillae aggregate laterally, smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 = A2, P1 = P2>P3; the upper jaw sheath is wide, M-shaped, and the lower jaw sheath is wide, V-shaped; the upper jaw sheath is slightly wider than the lower jaw sheath. Nares medium (ND/ED = 0.26–0.29), rounded, dorsally positioned. Eyes medium (ED/BH = 0.26–0.27), laterally positioned. Spiracle sinistral, medium to long (SL/BL = 0.18–0.24), wide (SW/BH = 0.25–0.26), opening at the posterior third of the body, posterodorsally directed, with centripetal wall fused to the body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.33–0.45). The dorsal fin is high (DFH/TMHW = 1.17–1.21), originating at the body with median slope, and convex margin; ventral fin is high (VFH/TMH = 0.98–1.02), with convex margin; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles analyzed in our study closely resemble those described by Cei (1980) and Pimenta et al. (2014), differing only by the elliptical body shape in dorsal view from those tadpoles described by Cei (1980), which was described as ovoid, but this difference represents a difference in terminology use. Tadpoles described by Bokermann (1967) had a different LTRF [2(1,2)/3(1)]. In our sample, one of the tadpoles had the A2 teeth row longer than the A1. Tadpoles of *S. squalirostris* were distinguished from tadpoles of *S. fuscovarius* because they were slender, had a rounded snout, and the origin of the dorsal fin is closer to the eyes. In addition, *S. squalirostris* could be distinguished from the tadpoles of *S. fuscomarginatus* by higher body and deeper dorsal and ventral fins. The snout rounded in lateral view differ *S. squalirostris* from *S. rupestris* and *Scinax* sp., and the oral disc ventrally emarginated differ *S. squalirostris* from *S. rupestris.* Tadpoles of *S. squalirostris* are smaller and had the P3 smaller when compared to *S. similis.*

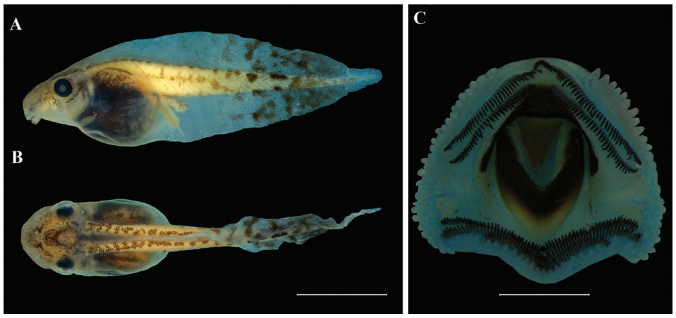

Figure 28. Tadpoles of *Scinax squalirostris* at Stage 35 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

Trachycephalus typhonius (Linnaeus 1758)

First Description of the tadpole: Vera Cruz – México (Pyburn 1967).

Other characterizations: Colômbia (Duellman 1970, 2005); Argentina (Cei 1980); Pará and Roraima, Brazil (Schiesari et al. 1996); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Bolivia (Schulze et al. 2015). Although lacking a formal characterization, some larval traits can be found in available taxonomic keys for the tadpoles from the Amazonas (Hero 1990) and Colombia (Lynch 2006).

Specimens Examined: Brazil, Goiás State, municipalities of Cidade de Goiás (ZUFG 1916, ZUFG 1927), Serranópolis (ZUFG 1371). Description based on 15 tadpoles between Gosner Stages 36 and 40.

Characterization. Total length 36.46 ± 4.02 mm (Table 1, Figure 29). The body shape is elliptical in dorsal view and triangular-compressed in lateral view (BW/BH = 0.95–0.98). The snout is sloped in lateral view. The oral disc is anteroventral, lateroventrally emarginate, with a biseriate row of elongated marginal papillae, interrupted by a dorsal gap; submarginal papillae aggregate laterally, smaller than the marginal papillae. LTRF is 4(1,3)/5(1), A1 = A2 = A3 = A4, P1 = P2 = P3 = P4 > P5 with the A4 row rather fragmented; accessory teeth rows presented laterally on the oral disc. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares medium (ND/ED = 0.20–0.28), rounded, dorsally positioned. Eyes medium (ED/BH = 0.17–0.18), laterally positioned. Spiracle sinistral, lateroventral, medium to long (SL/BL = 0.13–0.21), with medium width (SW/BH = 0.14–0.20), opening on the posterior third of the body, posterodorsally directed, with centripetal wall fused to the body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.32–0.34). The dorsal fin has medium height (DFH/TMH = 0.76–0.81), originating at the body with median slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.71–0.71) with convex margin; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles described by Schiesari et al. (1996) were larger (TL = 59.9 mm, Stages 39) than those in our sample. Tadpoles described by Duellman (2005) do not have submarginal papillae, but the author report the presence of small papillae positioned in the lateral folder, which could be a reference to the accessory teeth rows or o the

Figure 29. Tadpoles of *Trachycephalus typhonius* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

submarginal papillae. Cei (1980) reports for the tadpoles of Argentina a LTRF 2(2)/5(1), eventually with an additional P6, but generally, the P5 and P6 were highly fragmented whenever present. For Duellman (1970) and Rossa-Feres & Nomura (2006), the P6 teeth row was more common and the interruptions in the teeth rows had a different pattern, resulting in a LTRF of 4(1,2,4)/6(1,6). Schiesari et al. (1996) already described the variation in the number of teeth rows, suggesting that this variation could be related to the developmental stages, finding until nine posterior labial teeth rows in tadpoles of *T. typhonius*. In our sample, the LTRF showed large variation, with LTRF 4(1,3)/5(1) found in eight of the tadpoles, followed by the LTRF 3(1,3)/6(1), found in five of the tadpoles, and the LTRF 3(1)/5(1), found in one of the tadpoles. Whenever present, the row P6 was shorter than the other rows of labial teeth and fragmented and, as seen by Schiesari et al. (1996), was positioned next to the row of marginal papillae. Navarro-Acosta et al. (2017) studied the teeth row development of four tadpoles of anuran species from the *Boana pulchella* group and *B. faber* and found that rows were added distally in both labia. The same pattern was reported by Sánchez (2010) for Colombian *Hiloscirtus* species. Thus, despite lack of developmental studies of the oral disc in *Trachycephalus*, we suggest that is very likely that the formation of supernumerary rows follow the same patterns of development described by Navarro Acosta et al. (2017) and Sánchez (2010). The lateral line was evident in six individuals.

5. Leptodactylidae Werner 1896 (1838)

Leptodactylus fuscus (Schneider 1799)

First Description of the tadpole: French Guiana – SR (Lescure 1973).

Other characterizations: Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014); Bolivia (Schulze et al. 2015).

Specimens Examined: Brazil, Goiás State, municipality of São Miguel do Araguaia (ZUFG 1967). Description based on five tadpoles between Gosner Stages 36 and 37.

Characterization. Total length 29.32 ± 3.10 mm (Table 1, Figure 30). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.27–1.09). The snout is rounded in lateral view. The oral disc is anteroventral, not emarginate, with a uniseriate row of elongate marginal papillae, in alternate disposition, interrupted by a dorsal gap; submarginal papillae absent. LTRF is 2(2)/3, A1 slightly smaller than A2, P1 = P2 and P3 slightly smaller than P2. The upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares medium to large (ND/ED = 0.36–0.39), elliptical, dorsally positioned. Eyes medium (ED/BH = 0.17–0.17), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.10–0.18) and medium width (SW/BH = 0.13–0.17), opening on the middle third of the body, posterodorsally directed, with centripetal wall fused to the body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.27–0.41). The dorsal fin is low (DFH/TMH = 0.43–0.48), originating at the tail-body junction with acute slope, and convex margin; ventral fin is low (DFH/TMH = 0.41–0.43) with convex margin to the caudal musculature; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles described by Lescure (1973) have a biseriate row of marginal papillae (uniseriate in our sample), while the tadpoles analyzed by Rossa-Feres & Nomura (2006) had LTRF 2(2)/3(1). The absence of projection on the marginal rim and LTRF 2(2)/3 in our sample, resemble the populations analyzed by Pimenta et al. (2014). The populations described by Schulze et al. (2015), present a biseriate marginal papillae ventrally and LTRF 2(2)/3(1). In our sample, one individual presented the A1 teeth row with the same length than A2.

Leptodactylus labyrinthicus (Spix 1824)

First Description of the tadpole: Guapiaçu – SP, Brazil (Vizotto 1967).

Other characterizations: São José do Rio Preto – SP, Brazil (Rossa-Feres & Nomura 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014).

Specimens Examined: Brazil, Goiás State, municipalities of Caiapônia (ZUFG 2028), Rio Verde (ZUFG 664). Description based on eight tadpoles between Gosner Stages 35 and 40.

Characterization. Total length 58.72 ± 5.13 mm (Table 1, Figure 31). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.15–1.18). The snout is rounded in lateral view. The oral disc is anteroventral, not emarginate, with a uniseriate row of short and rounded marginal papillae, alternated ventrally, interrupted by a dorsal gap; submarginal papillae absent. LTRF is 1/2(1), P1 slightly smaller than P2; the upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper and lower jaw sheath have the same width. Nares medium to large (ND/ED = 0.35–0.38), elliptical, dorsally positioned. Eyes small to medium (ED/BH = 0.14–0.17), dorsally positioned. Spiracle sinistral, medium to long (SL/BL = 0.13–0.21), wide width (SW/BH = 0.29–0.35), opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.46–0.46).

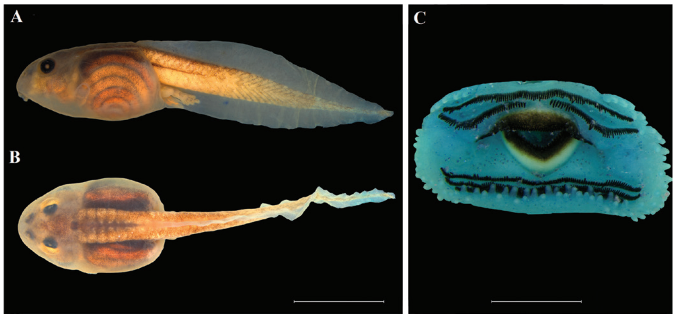

Figure 30. Tadpoles of *Leptodactylus fuscus* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

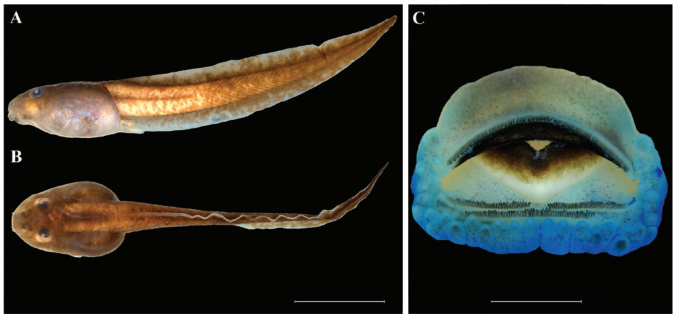

Figure 31. Tadpoles of *Leptodactylus labyrinthicus* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

The dorsal fin is low (DFH/TMH = 0.34–0.45), originating on the posterior third of the body with acute slope, and margin parallel to the caudal musculature; ventral fin is low (VFH/TMH = 0.36–0.40) with margin parallel to the caudal musculature; the tail tip is pointed; tail very long, with almost four to five times the body length. Lateral line evident.

Comments. Tadpoles analyzed by Vizotto (1967) were larger (TL = 75 mm, Stages 39, TL = 58.72 mm, Stages 35–40, in our sample), and the tadpoles described by Rossa-Feres & Nomura (2006) were smaller (TL = 48.10 mm, Stages 36–39). Tadpoles analyzed by Rossa-Feres & Nomura (2006) also had the oral disc emarginate ventrally and with uniseriate marginal papillae. From the total of analyzed individuals, four individuals had uniseriate marginal papillae, one had the oral disc ventrally directed. Tadpoles of *L. labyrinthicus* were easily differentiated from those of *L. fuscus* by the larger total length (TL = 29.32 mm, Stages 36–37, in *L. fuscus*; TL = 58.72 mm, Stages 35–40, in *L. labyrinthicus*), smaller body when compared to the tail length and teeth row formula 1/2(1) in *L. labyrinthicus* and 2(2)/3 in *L. fuscus*.

Leptodactylus luctator (Hudson 1892)

First Description of the tadpole: Argentina (Fernandez & Fernandez, 1921).

Other characterizations: São Paulo, Brazil (Rosa, 1965); Argentina (Cei, 1980); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura, 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014). Although lacking a formal characterization, some larval traits can be found in available taxonomic key for the tadpoles from the Amazonas (Hero 1990).

Specimens Examined: Brazil, Goiás State, municipalities of Cidade de Goiás (ZUFG 1915), Cristalina (ZUFG 1410), Jataí (ZUFG 1228), Rio Verde (ZUFG 165). Description based on 13 tadpoles between Gosner Stages 35 and 40.

Characterization. Total length 45.30 ± 7.73 mm (Table 1, Figure 32). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 0.46–1.07). The snout is rounded in lateral view. The oral disc is anteroventral, ventrally folded, with a biseriate row of elongate marginal papillae ventrally and triseriate laterally, interrupted by a dorsal gap; submarginal papillae absent. LTRF is 2/3, A1 = A2, P1 = P2, P3 slightly smaller than P2. The upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper and lower jaw sheaths were of the same width. Nares large (ND/ED = 0.41–0.42), elliptical, with a small projection on marginal rim, dorsolaterally positioned. Eyes small (ED/BH = 0.11–0.13), dorsally positioned. Spiracle sinistral, lateroventral, with median length (SL/BL = 0.14–0.15), medium to wide (SW/BH = 0.20–0.26), opening at the middle third of the body, posterodorsally directed, with the centripetal wall fused to body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.32–0.42). The dorsal fin has medium height (DFH/TMHW = 0.56–0.64), originating at the tail-body junction with acute slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.51–0.68) with convex margin; the tail tip is rounded. Lateral line evident.

Comments. Recently, Magalhães et al. (2020) revised the taxonomy of *L. latrans* species group, defining the *L. latrans* species as endemic of Atlantic Forest, attributing the name *L. luctator* to the lineages of (formerly known as) *L. latrans* in the Cerrado, southern Brazil, southeastern Paraguay, Argentina, and Uruguay. Tadpoles from our sampled population were smaller than the tadpoles described by Fernandez & Fernandez (1921) (TL = 73 mm, probably Stages 39), and Rosa (1965) (TL = 90 mm) but were of similar size when compared to the tadpoles described by Rossa-Feres & Nomura (2006). From the total of analyzed individuals, two presented a snout sloped in lateral view, one had P1 = P2, one individual had the marginal papillae uniseriate ventrally, and another individual had the marginal papillae biseriate. The teeth row formula, larger total length, elongated body shape in dorsal view, and the marginal papillae biseriate ventrally and triseriate laterally in *L. luctator*, differ *L. luctator* tadpoles of *L. fuscus* and *L. labyrinthicus.*

Leptodactylus podicipinus (Cope 1862)

First Description of the tadpole: Ibirá – SP, Brazil (Vizotto 1967).

Other characterizations: Trinidad and Tobago (Kenny 1969); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Bolívia (Schulze et al. 2015).

Specimens Examined: Brazil, Goiás State, municipality of Iporá (ZUFG 2268). Description based on three tadpoles between Gosner Stages 31 and 37.

Characterization. Total length 24.03 ± 1.09 mm (Table 1, Figure 33). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.15–1.19). The snout is sloped in lateral view. The oral disc is anteroventral, ventrally folded, with a uniseriate row of elongated marginal papillae laterally, biseriate lateroventrally, interrupted by dorsal gap; three submarginal papillae laterally. LTRF is 2/3, A1 = A2, P1 = P2, P3 slightly smaller than P2. The upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares large to very large (ND/ED = 0.45–0.56), elliptical,

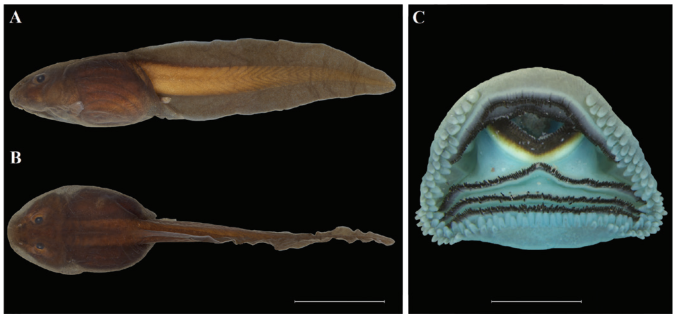

Figure 32. Tadpoles of *Leptodactylus latrans* at Stage 34 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 39 (scale 2 mm).

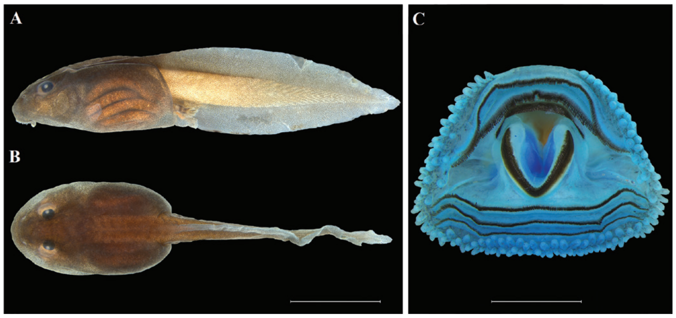

Figure 33. Tadpoles of *Leptodactylus podicipinus* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

dorsally positioned. Eyes small to medium (ED/BH = 0.12–0.17), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.09–0.13) and medium width (SW/BH = 0.16–0.24), opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to the body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.32–0.36). The dorsal fin has medium height (DFH/TMH = 0.67–0.71), originating on the posterior third of the body with a median slope, with convex margin; ventral fin has medium height (VFH/TMH = 0.61–0.61) with convex margin; the tail tip is rounded. Lateral line not evident.

Comments. Tadpoles in our sample (TL = 24.03 mm, Stages 31–37) were smaller than the tadpoles described by Vizotto (1967) (TL = 30 mm, Stage 39) and by Kenny (1969) (TL = 35 mm, about Stage 30), but larger than the tadpoles described by Rossa-Feres & Nomura (2006) (TL = 25.03 mm, Stage 37) and Schulze *et al.* (2015) (TL = 23.70 mm, Stage 36). Tadpoles described by Kenny (1965) also differ by the presence of a ventral gap on the row of marginal papillae, and by having the ventral marginal papillae shorter than the lateral marginal papillae. The populations analyzed by Rossa-Feres & Nomura (2006) have the marginal papillae triseriate laterally. Tadpoles described by Schulze *et al.* (2015) differ from our samples by oral disc described as not emarginated, LTRF 2(2)/3, marginal papillae biseriate laterally, and biseriate to triseriate ventrally, and A1 slightly shorter than A2. From the total of analyzed individuals, one individual has snout slightly sloped and one individual does not have submarginal papillae. Tadpoles of *L. podicipinus* can be distinguished of those of *L. fuscus*, *L. luctator*, e *L. labyrinthicus*, by lower total length (24.03 mm in *L. podicipinus*, stages 31 and 37, 29.32 mm in *L. fuscus*, stages 36 and 37, 45.30 mm in and *L. luctator*, stages 35 and 40, 58.72 mm in *L. labyrinthicus*, stages 35 and 40), and by the teeth row formula (LTRF 2/3 in *L. podicipinus*, 2(2)/3 in *L. fuscus* and *L. labyrinthicus*).

Leptodactylus troglodytes Lutz 1926

First Description of the tadpole: Cabeceiras – PB, Brazil (Cascon & Peixoto 1985).

Other characterizations: Not available.

Specimens Examined: Brazil, Tocantins State, Parque Estadual do Lajeado (ZUFG 2947). Description based on three tadpoles between Gosner Stages 31 and 37.

Characterization. Total length 35.77 ± 3.23 mm (Table 1, Figure 34). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.15–1.25). The snout is sloped in lateral view. The oral disc is ventral, not emarginate, with a uniseriate row of elongated marginal papillae, with alternated disposition, interrupted by dorsal gap; submarginal papillae absent. LTRF is 2(2)/3, A1 slightly smaller than A2, P1 = P2, P2 slightly smaller than P3. The upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower. Nares medium to large (ND/ED = 0.33–0.50), elliptical, dorsolaterally positioned. Eyes small (ED/BH = 0.14–0.14), dorsally positioned. Spiracle sinistral, lateroventral, with medium length (SL/BL = 0.14–0.16) and medium width (SW/BH = 0.16–0.22), opening on the posterior third of the body, posterodorsally directed, centripetal wall fused to body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMH/BW = 0.31–0.32). The dorsal fin is low to medium (DFH/TMH = 0.47–0.70), originating on the posterior third of the body with a median slope, and margin parallel to the caudal musculature; ventral fin has medium height (VFH/TMH = 0.51–0.64) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line not evident.

Comments. Tadpoles described by Cascon & Peixoto (1985) were larger (TL = 43 mm, Stage 36) than the tadpoles included in our sample. In our sample, one individual had the A1 with the same length of the A2. Tadpoles of *L. troglodytes* (TL = 35.77 mm, Stages 34–38) were smaller than the tadpoles of *L. labyrinthicus* (TL = 58.72 mm, Stages 35–40) and *L. luctator* (TL = 45.30 mm, Stages 35–40), but larger than tadpoles of *L. podicipinus* (TL = 24.03 mm, Stages 31–37). The teeth row formula of *L. troglodytes* [2(2)/3] also differ from the LTRF of *L. luctator* (2/3) and the sloped snout in lateral view differ from the snout of *L. fuscus*.

Physalaemus centralis Bokermann 1962

First Description of the tadpole: Nova Aliança – SP, Brazil (Rossa-Feres & Jim 1993).

Other characterizations: Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Bolívia (Schulze et al. 2015). Although lacking a formal characterization, some larval traits can be found in Ruggeri & Weber (2012).

Specimens Examined: Brazil, Goiás State, municipality of Aruanã (ZUFG 571, ZUFG 582). Description based on ten tadpoles between Gosner Stages 37 and 40.

Characterization. Total length 23.18 ± 1.89 mm (Table 1, Figure 35). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.09–1.23). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of elongated marginal papillae, interrupted by one dorsal and two lateroventral gaps (type C1 *sensu* Vera Candioti *et al.* 2011); submarginal papillae absent. LTRF is 2(2)/2, with A1 = A2, P1 slightly smaller than P2. The upper

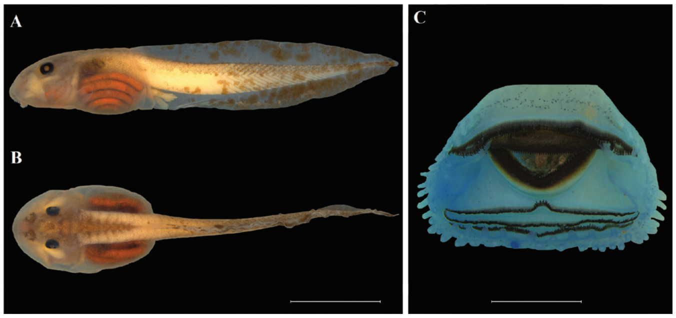

Figure 34. Tadpoles of *Leptodactylus troglodytes* at Stage 37 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

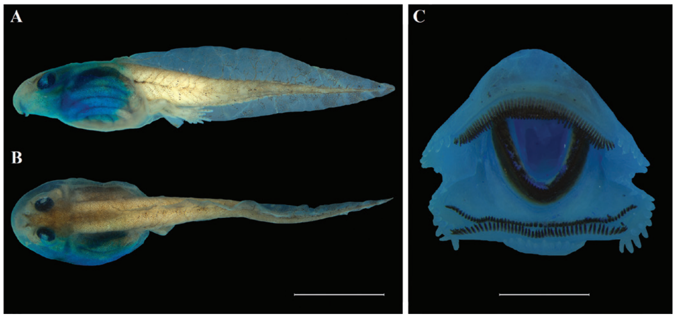

Figure 35. Tadpoles of *Physalaemus centralis* at Stage 39 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 38 (scale 2 mm).

jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the lower jaw sheath is wider than the upper jaw sheath. Nares medium (ND/ED = 0.32–0.36), elliptical, with a small projection on marginal rim, dorsally positioned. Eyes medium (ED/BH = 0.22–0.22), dorsally positioned. Spiracle sinistral, lateroventral, medium to long (SL/BL = 0.07–0.25), wide (SW/BH = 0.27–0.28), opening on the middle third of the body, ventrally directed, with the centripetal wall totally fused to body wall. Vent tube medial, with free distal edge. The caudal musculature width is medium (TMW/BW = 0.35–0.40). The dorsal fin has low to medium height (DFH/TMH = 0.42–0.63), originating on the posterior third of the body with median slope, and convex margin; ventral fin is low (VFH/TMH = 0.23–0.42) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles described by Rossa-Feres & Jim (1993), Rossa-Feres & Nomura (2006) (TL = 20.20 mm, Stage 37) and the morphotype *P. centralis* A described by Schulze et al. (2015) (TL = 15 mm, Stages 26-27) were smaller than our tadpoles (TL = 23.18 mm, Stages 37–40). The *P. centralis* A morphotype (Schulze et al. 2015) also differ from our tadpoles by having a ventral emargination, LTRF 2(2)/3(1), nares with a prominent projection on the marginal rim, and spiracle not fused to body and directed posteriorly. The presence of lateroventral gap in the oral disc (C1 type *sensu* Vera Candioti et al. 2011) and the total length of 21.40 mm, in Stage 39, makes the *P. centralis* B morphotype (Schulze et al. 2015) like those tadpoles previously described, being little smaller than tadpoles analyzed in our study, but differ by the LTRF 2(2)/3(1), spiracle not fused to body and directed posterodorsally. From the total of analyzed individuals, one individual had submarginal papillae scattered lateroventrally, two had the upper jaw sheath in M- shaped, and one individual had one ventral gap.

Physalaemus cuvieri Fitzinger, 1826

First Description of the tadpole: São Paulo, Brazil (Bokermann, 1962).

Other characterizations: Argentina (Cei, 1980); Boracéia – SP, Brazil (Heyer et al. 1990); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura, 2006); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014). Although lacking a formal characterization, some larval traits can be found in available in Ruggeri & Weber (2012).

Specimens Examined: Brazil, Goiás State, municipality of Alto Paraíso (ZUFG 1121), Aparecida do Rio Doce (ZUFG 1842), Cocalzinho (ZUFG 174), Corumbá (ZUFG 47), Serranópolis (ZUFG 92), and Tocantins State, Parque Estadual do Lajeado (ZUFG 2519). Description based on 15 tadpoles between Gosner Stages 34 and 38.

Characterization. Total lengths 20.85 ± 2.54 mm (Table 1, Figure 36). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.06–1.27). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of elongated marginal papillae, interrupted by one dorsal, one ventral and two lateroventral ventral gaps (C4 type *sensu* Vera Candioti et al. 2011), submarginal papillae absent. LTRF is 2(2)/3(1), with the A1 slightly smaller than the A2, P1>P2 and P3 with a third the length of the P2. The upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the lower jaw sheath is wider than the upper jaw sheath. Nares very large (ND/ED = 0.80–0.85), elliptical, with a small projection on marginal rim, dorsally positioned. Eyes small (ED/BH = 0.15–0.16), dorsally positioned. Spiracle sinistral, medium to long (SL/BL = 0.19–0.24), with medium width (SW/BH = 0.19–0.20), with opening on the posterior third of the body, posterodorsally directed, with the centripetal wall fused to body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.33–0.33). The dorsal fin has medium height (DFH/TMH = 0.50–0.73), originating on the posterior third of the body with median slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.32–0.52) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line not evident.

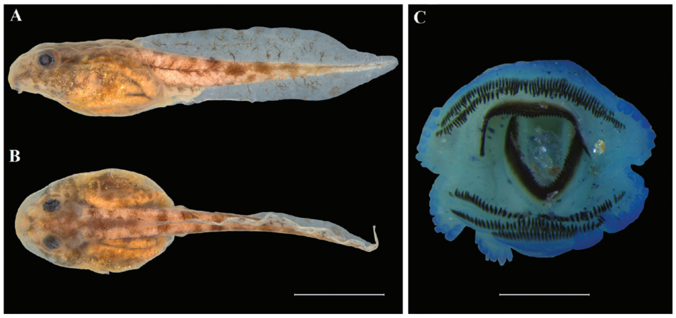

Figure 36. Tadpoles of *Physalaemus cuvieri* at Stage 37 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

Comments. Tadpoles described by Bokermann (1962) and Cei (1980) differ from those studied herein by the LTRF 2/3(1). Tadpoles in our sample were larger than those analyzed by Heyer (1990) (TL = 23.30 mm, Stage 34) and Rossa-Feres & Nomura (2006) (23.49 mm, Stages 34–39). From the total of analyzed individuals, three had the LTRF 2/3(1), four had the A1 with the same length than the A2, five had one or two submarginal papillae laterally (from which one had accessory teeth row), and six individuals had the upper jaw sheath M-shaped. The presence of marginal rim also varies, with three tadpoles with a small projection on the marginal rim, and three tadpoles presented the marginal rim in only one nare. Tadpoles of *P. cuvieri* are easily differentiated from those of *P. centralis* by the LTRF 2(2)/3(1), larger nares (average of 1.01 mm in diameter for *P. cuvieri*, and 0.53 mm for *P. centralis*), and by the spiracle posterodorsally directed.

Physalaemus marmoratus (Reinhardt & Lütken 1862)

First Description of the tadpole: Argentina (Cei 1980).

Other characterizations: Nova Itapirema – SP, Brazil (Nomura et al. 2003), Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Bolívia (Schulze et al. 2015).

Specimens Examined: Brazil, Goiás State, municipalities of Aparecida do Rio Doce (ZUFG 2521), Aruanã (ZUFG 600), Barro Alto (ZUFG 847). Description based on eight tadpoles between Gosner Stages 35 and 40.

Characterization. Total lengths 23.76 ± 1.47 mm (Table 1, Figure 37). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.12–1.15). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of elongated marginal papillae, interrupted by one dorsal gap (C2 type *sensu* Vera Candioti et al. 2011); submarginal papillae absent. LTRF is 2(2)/2(1), A1 is slightly smaller than A2, P1 is slightly wider than P2. The upper jaw sheath is narrow to medium, M-shaped, and the lower jaw sheath is narrow, V-shaped; the upper

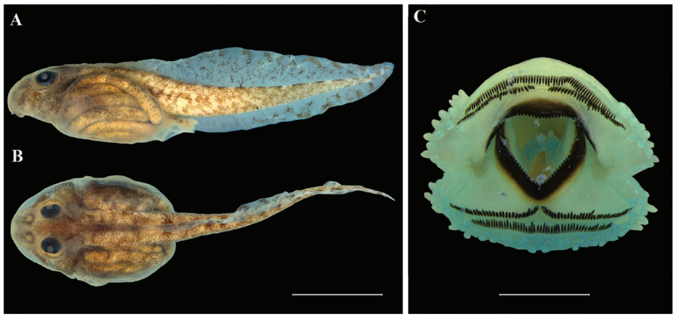

Figure 37. Tadpoles of *Physalaemus marmoratus* at Stage 35 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

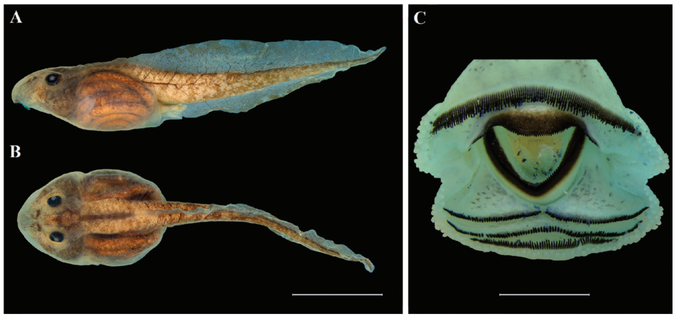

Figure 38. Tadpoles of *Physalaemus nattereri* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

jaw sheath is wider than the lower jaw sheath. Nares large to very large (ND/ED = 0.47–0.56), rounded, with a very small projection on the marginal rim, dorsally positioned. Eyes small to medium (ED/BH = 0.15–0.19), dorsally positioned. Spiracle sinistral, medium to long (SL/BL = 0.15–0.21), with medium width (SW/BH = 0.20–0.22), with opening on the middle third of the body, posterodorsally directed, centripetal wall fused to body wall. Vent tube medial fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.33–0.37). The dorsal fin has medium height (DFH/TMH = 0.52–0.61), originating on the posterior third of the body with acute slope, and convex margin; ventral has low to medium height (VFH/TMH = 0.42–0.45) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles analyzed by Rossa-Feres & Nomura (2006) differ from those in our sample by the uniseriate marginal papillae and smaller size (TL = 32.64 mm, Stages 35–39, Rossa-Feres & Nomura 2006; TL = 33.84 mm, Stages 34–37, our sample). Tadpoles were described by Rossa-Feres & Nomura (2006) as having the P2 teeth row slightly longer than the P1 and the P3, but figure shows the P1 teeth row and the P2 of similar sizes, and both longer than the P3. The populations described by Schulze et al. (2015) were smaller (TL = 31.3 mm in Stages 37–41), had a uniseriate marginal papilla, and the P1 teeth row slightly smaller than the P2 and the P3. Three individuals in our sample had the uniseriate marginal papillae in alternated disposition laterally, two individuals had the marginal papillae uniseriate lateroventrally, and one individual had the marginal papillae biseriate laterally. In one individual, the A1 teeth row had the same length than the A-2 and five individuals presented the upper jaw sheath M-shaped. Tadpoles of *P. marmoratus* were easily differentiated from those of *P. centralis* and *P. cuvieri*, by the absence of a ventral gap. The spiracle posterodorsally directed differentiates *P. marmoratus* from *P. centralis* (ventrally directed).

Physalaemus nattereri (Steindachner 1863)

First Description of the tadpole: São José do Rio Preto – SP, Brazil (Vizotto 1967).

Other characterizations: Argentina (Cei 1980); Nova Itapirema – SP, Brazil (Rossa-Feres & Nomura 2006); Bolívia (Schulze et al. 2015).

Specimens Examined: Brazil, Goiás State, municipalities of Aparecida do Rio Doce (ZUFG 1817, ZUFG: 1839), Chapadão do Céu (ZUFG: 1347, ZUFG: 1958), Cidade de Goiás (ZUFG: 1921). Description based on 13 tadpoles between Gosner Stages 34 and 37.

Characterization. Total length 33.84 ± 3.10 mm (Table 1, Figure 38). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.18–1.21). The snout is sloped in lateral view. The oral disc is anteroventral, laterally emarginate, with uniseriate row of elongated marginal papillae ventrally, in alternated disposition, biseriate lateroventrally, interrupted by a dorsal gap; submarginal papillae absent. LTRF is 2(2)/3(1), with A1 teeth row slightly longer than A2, P1 slightly longer than P2 and P3 slightly shorter than P2. The upper jaw sheath is wide, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper and lower jaw sheath had the same width. Nares large (ND/ED = 0.41–0.49), rounded, dorsally positioned. Eyes small to medium (ED/BH = 0.14–0.18), dorsally positioned. Spiracle sinistral, medium to long (SL/BL = 0.12–0.22), with medium width (SW/BH = 0.15–0.20), opening on the posterior third of the body, posterodorsally directed, with the centripetal wall fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.31–0.36). The dorsal fin has medium height (DFH/TMH = 0.53–0.67), originating on the posterior third of the body with a median slope, with a convex margin; ventral fin has low to medium height (VFH/TMH = 0.29–0.44) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line not evident.

Comments. Tadpoles analyzed by Rossa-Feres & Nomura (2006) differ from those in our sample by the uniseriate marginal papillae and smaller size (TL = 32.64 mm, Stages 35–39, Rossa-Feres & Nomura 2006; TL = 33.84 mm, Stages 34–37, our sample). Tadpoles were described by Rossa-Feres & Nomura (2006) as having the P2 teeth row slightly longer than the P1 and the P3, but figure shows the P1 teeth row and the P2 of similar sizes, and both longer than the P3. The populations described by Schulze et al. (2015) were smaller (TL = 31.3 mm in Stages 37–41), had a uniseriate marginal papilla, and the P1 teeth row slightly smaller than the P2 and the P3. Three individuals in our sample had the uniseriate marginal papillae in alternated disposition laterally, two individuals had the marginal papillae uniseriate lateroventrally, and one individual had the marginal papillae biseriate laterally. In one individual, the A1 teeth row had the same length than the A-2 and five individuals presented the upper jaw sheath M-shaped. Tadpoles of *P. nattereri* were easily differentiated from those of *P. centralis*, *P. cuvieri*, and *P. marmoratus* by the absence of a ventral gap.

6. Microhylidae Günther 1858

Chiasmocleis albopunctata (Boettger 1885)

First Description of the tadpole: Uberlândia – MG, Brazil (Oliveira-Filho & Giaretta 2006).

Other characterizations: Bolivia (Schulze et al. 2015).

Specimens Examined: Brazil, Goiás State, Parque nacional da Chapada dos Veadeiros National (ZUFG 2294, ZUFG 2948). Description based on six tadpoles between Gosner Stages 35 and 40.

Characterization. Total length 20.25 ± 2.65 mm (Table 1, Figure 39). The body shape is rounded in dorsal view and triangular-depressed in lateral view (BW/BH = 1.01–1.19). The snout is truncate in lateral view. Oral disc without keratinized mouthparts or papillae; presence of a dermal flap suspended in front of oral cavity. Nares not perforated. Eyes medium (ED/BH = 0.22–0.22), laterally positioned. Spiracle ventral, with medium length (SL/BL = 0.12–0.16), medium to wide (SW/BH = 0.24–0.30), opening on the posterior third of the body, covering the vent tube in three of six tadpoles but anterior to the vent tube in three of six tadpoles, posteriorly directed, with the centripetal wall not fused to the body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.27–0.38), with the anterior third of the tail muscle and adjacent fins with a sheath of thick connective tissue. The dorsal fin has medium height (DFH/TMH = 0.51–0.81), originating on the posterior third of the body with median slope, with a convex margin; ventral fin has medium height (VFH/TMH = 0.61–0.91) with a convex margin; the tail tip end with a flagellum. Lateral line evident.

Comments. Tadpoles analyzed by Schulze et al. (2015) were smaller (TL = 17.7 mm, Stages 35–39), and were described as having a rounded snout. In three of six individuals in our sample, the spiracle was not long enough to cover the vent tube and in one of six individuals, the vent tube was dextral.

Dermatonotus muelleri (Boettger 1885)

First Description of the tadpole: Santa Fé do Sul – SP (Vizotto 1967).

Other characterizations: Argentina (Cei 1980, Lavilla 1992); Vitória Brasil – SP, Brazil (Rossa-Feres & Nomura 2006); Bolivia (Schulze et al. 2015). Information about the larval development for populations from Argentina were presented by Fabrezi et al. (2012).

Specimens Examined: Brazil, Goiás State, municipalities of Britânia (ZUFG 1940), Pontalina (ZUFG 1283, ZUFG 1304), Nova Roma (ZUFG: 1955), and Mato Grosso do Sul State, municipality of São Gabriel do Oeste (ZUFG 1956). Description based on 15 tadpoles between Gosner Stages 31 and 37.

Characterization. Total length 36.45 ± 3.62 mm (Table 1, Figure 40). The body shape is rounded in dorsal view and triangular-depressed in lateral view (BW/BH = 1.21–1.32). The snout is rounded in lateral view. Oral disc modified without keratinized mouthparts or papillae; presence of a dermal flap suspended in front of oral cavity. Nares not perforated. Eyes medium (ED/BH = 0.16–0.18), laterally positioned. Spiracle ventral, long (SL/BL = 0.22–0.28), narrow to medium (SW/BH = 0.07–0.10), opening on the posterior third of the body, covering the vent tube, posteriorly directed, with the centripetal wall not fused with the body wall. Vent tube medial, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.28–0.36), with the anterior third of the tail muscle and adjacent fins with a sheath of thick connective tissue. The dorsal fin has medium height (DFH/TMH = 0.64–0.75), originating at the body-tail junction with acute slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.64–0.84) with convex margin; the tail tip is pointed. Lateral line evident.

Comments. Vizotto (1967) considered the tadpoles to have large eyes while Cei (1980) and Lavilla (1992) described the eyes of the tadpoles as small. Tadpoles in our sample are like those described by Rossa-Feres & Nomura (2006). In two individuals in our sample, the spiracle was not long enough to cover the vent tube. Tadpoles of *D. muelleri* were easily differentiated from those of *C. albopunctatus* by the larger total length and the rounded snout in lateral view.

Elachistocleis cesarii (Miranda-Ribeiro 1920)

First Description of the tadpole: Mirassol – SP, Brazil (Rossa-Feres & Nomura 2006).

Other characterizations: Macaíba – SP, Brazil (Magalhães et al. 2012)

Specimens Examined: Brazil, Goiás State, municipalities of Barro Alto (ZUFG 891, ZUFG 892), Britânia (ZUFG 1939), Cidade de Goiás (ZUFG: 1920), São João d'Aliança (ZUFG 1098, ZUFG 1101), São Miguel do Araguaia (ZUFG 1886). Description based on 14 tadpoles between Gosner Stages 35 and 38.

Characterization. Total length 26.94 ± 4.27 mm (Table 1, Figure 41). The body shape is rounded in dorsal view and triangular-depressed in lateral view (BW/BH = 1.41–1.72). The snout is truncate in lateral view. Oral disc modified without keratinized mouthparts or papillae; presence of paired dermal flaps suspended in front of oral cavity; dermal flaps with irregular edges. Nares not perforated. Eyes small (ED/BH = 0.16–0.17), laterally positioned. Spiracle ventral, with medium length (SL/BL = 0.14–0.19) and medium width (SW/BH = 0.12–0.17), opening on the posterior to the body, covering the vent tube, posteriorly directed, with the centripetal wall not fused with the body wall. Vent tube medial with sinistral opening, fused to the ventral fin. The caudal musculature

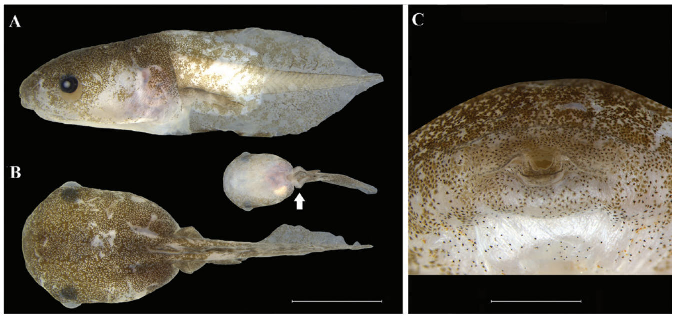

Figure 39. Tadpoles of *Chiasmocleis albopunctata* at Stage 39 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm). The arrow indicates the spiracle position.

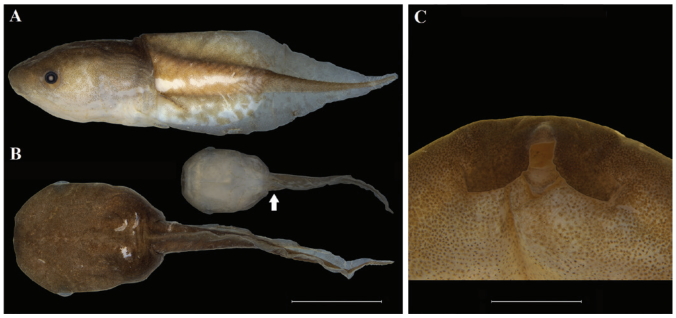

Figure 40. Tadpoles of *Dermatonotus muelleri* at Stage 39 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm). The arrow indicates the spiracle position.

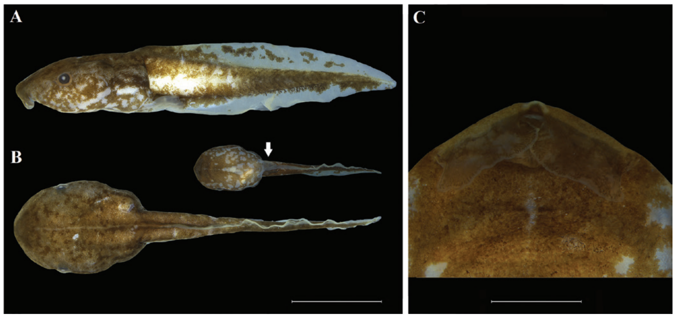

Figure 41. Tadpoles of *Elachistocleis cesarii* at Stage 38 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm). The arrow indicates the spiracle position.

width is medium (TMW/BW = 0.28–0.34). The dorsal fin has medium height (DFH/TMH = 0.47–0.53), originating at the posterior third of the body with median slope, with convex margin; ventral fin has low to medium height (VFH/TMH = 0.30–0.51) with convex margin; the tail tip is rounded. Lateral line not evident.

Comments. The populations analyzed by Rossa-Feres & Nomura (2006) were like the tadpoles in our descriptions. The populations analyzed by Magalhães et al. (2012) differ from those in our sample herein by the vent tube with medial opening. The vent tube with sinistral opening and the presence of two labial flaps differ *E. cesarii* from *C. albopunctatus* and *D. muelleri*.

7. Odontophrynidae Lynch 1969

Odontophrynus cf. *juquinha*

First Description of the tadpole: species uncertain.

Other characterizations: not available.

Specimens Examined: Brazil, Minas Gerais State, municipality of Andradas (ZUFG 908). Description based on three tadpoles at Gosner Stage 37.

Characterization. Total length 41.43 ± 6.86 mm (Table 1, Figure 42). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.11–1.31). The snout is rounded in lateral view. The oral disc is anteroventral, laterally emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae scattered laterally, smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 = A2; P1 = P2 > P3. The upper jaw sheath is wide, arc-shaped, and the lower jaw sheath is wide, U-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares large to very large (ND/ED = 0.38–0.55), elliptical, with a small projection on the marginal rim, dorsally positioned. Eyes small (ED/BH = 0.09–0.14), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.08–0.09), narrow to medium (SW/BH = 0.09–0.11), opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to body wall and free distal edge. Vent tube with dextral opening, fused to the ventral fin. The caudal musculature width is narrow to medium (TMW/BW = 0.29–0.32). The dorsal fin is medium to high (DFH/TMH = 0.94–1.05), originating on the posterior third of the body with an acute slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.60–0.65) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line evident.

Comments. After Martino *et al.* (2019), the *O. americanus* species was restricted to southern Brazil, but these authors did not define a possible name for populations outside this distribution. As our sampled populations were geographically close to the *O. juquinha* (Rocha *et al.* 2017), we suspected that this species could have a larger geographical distribution. Our sample is like those described by Rocha *et al.* (2017) but our tadpoles have a larger total length.

Odontophrynus cultripes (Reinhardt & Lütken 1862)

First Description of the tadpole: Belo Horizonte – MG, Brazil (Savage & Cei 1965).

Other characterizations: Argentina (Cei 1980); Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014).

Specimens Examined: Brazil, Goiás State, municipality of Teresópolis (ZUFG 533). Description based on 14 tadpoles between Gosner Stages 35 and 38.

Characterization. Total length 34.87 ± 2.23 mm (Table 1, Figure 43). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.46–1.51). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae scattered lateroventrally, smaller than the marginal papillae. LTRF is 2(2)/3(1), A1<A2, P1>P2>P3. The upper jaw sheath is wide, arc-shaped, and the lower jaw sheath is wide, U-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares medium (ND/ED = 0.27–0.29), elliptical, with a projection on marginal rim, dorsally positioned. Eyes medium (ED/BH = 0.22–0.24), dorsally positioned. Spiracle sinistral, short (SL/BL = 0.06–0.06), narrow to medium (SW/BH = 0.08–0.13), opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to body wall and free distal edge. Vent tube

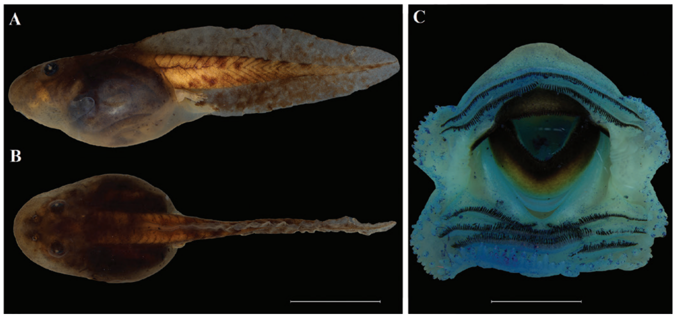

Figure 42. Tadpoles of *Odontophrynus* sp. (cf. *juquinha*) at Stage 38 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

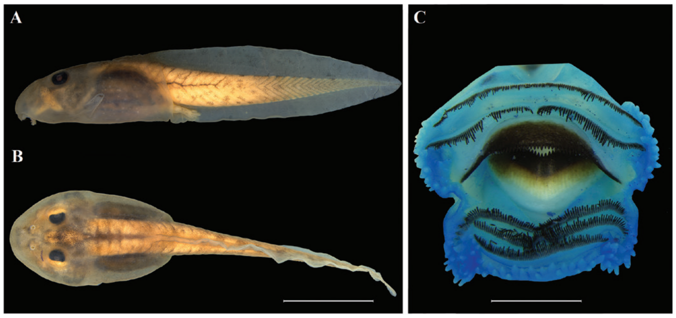

Figure 43. Tadpoles of *Odontophrynus cultripes* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

medial, with dextral opening, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.36–0.40). The dorsal fin has medium height (DFH/TMH = 0.61–0.61), originating at the body with an acute slope, with convex margin; ventral fin has medium height (VFH/TMH = 0.45–0.46) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line not evident.

Comments. Tadpoles described by Savage & Cei (1965) were smaller (TL = 14 mm, Stage 37) than the tadpoles in our samples (TL = 38.01 mm, Stages 35–38). Tadpoles of *O. cultripes* can be distinguished from tadpoles of *O. americanus* by being smaller and the elliptical body shape in dorsal view.

Odontophrynus sp.

First Description of the tadpole: Not applicable.

Other characterizations: not available.

Specimens Examined: Brazil, Goiás State, municipality of Alto Paraíso (ZUFG 1892). Description based on four tadpoles between Gosner Stages 31 and 40.

Characterization. Total length 53.51 ± 2.84 mm (Table 1, Figure 44). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.06–1.14). The snout is rounded in lateral view. The oral disc is anteroventral, laterally emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae absent. LTRF is 2(2)/3(1), A1 = A2, P1 = P2>P3; The upper jaw sheath is wide, M-shaped, and the lower jaw sheath is wide, U-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares small (ND/ED = 0.12–0.14), elliptical, with a small projection on the marginal rim, dorsally positioned. Eyes small (ED/BH = 0.15–0.16), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.09–0.10), narrow to medium (SW/BH = 0.09–0.10), opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to the body wall and free distal edge. Vent tube medial with dextral opening, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.32–0.32). The dorsal fin has medium height (DFH/TMH = 0.81–0.97), originating at the posterior third of the body with acute slope, with convex margin; ventral fin has medium height (VFH/TMH = 0.68–0.76) with convex margin; the tail tip is rounded. Lateral line not evident.

Comments. We are unable to associate this morphotype to other *Odontophrynus* species. Tadpoles of *Odontophrynus* sp. differ from the *O.* cf. *juquinha*, and *O. cultripes* by the upper jaw sheath M-shaped and larger total length. One individual presented one submarginal papilla on each side of the oral disc.

Proceratophrys boiei (Wied 1825)

First Description of the tadpole: Teresópolis – RJ, Brazil (Izeckson et al. 1979).

Other characterizations: Eastern Region of the Meridional Espinhaço Ridge – MG, Brazil (Pimenta et al. 2014).

Specimens Examined: Brazil, Minas Gerais State, municipality of Divino (ZUFG 2337). Description based on three tadpoles at Gosner Stage 31.

Characterization. Total length 32.39 ± 0.55 mm (Table 1, Figure 45). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.05–1.07). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae distributed laterally, forming rows, and smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 = A2, P1 slightly smaller than P2 and P2>P3. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the lower jaw sheath is wider than the upper jaw sheath. Nares large (ND/ED = 0.41–0.42), elliptical, with a projection on the marginal rim, dorsally positioned. Eyes small (ED/BH = 0.15–0.16), dorsally positioned. Spiracle sinistral, with medium length (SL/BL = 0.09–0.09), narrow to medium (SW/BH = 0.08–0.10), opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to the body wall and free distal edge. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.31–0.31). The dorsal fin is medium to high (DFH/TMH = 0.95–1.03), emerging at the tail-body junction with median slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.71–0.73) with margin parallel to the caudal musculature; the tail tip acute. Lateral line evident.

Comments. Tadpoles treated as *Stombus boiei* by Miranda-Ribeiro (1937) but the tadpoles presented in the Figure 5 is not representatives of the species (Izeckson et al. 1979). Tadpoles described by Izeckson et al. (1979) were like those in our sample but lacks the folds in the lower labium. From the total of analyzed individuals, one presented an elliptical body shape in dorsal view, and one individual had the A2 slightly longer than A1.

Proceratophrys cururu Eterovick & Sazima, 1998

First Description of the tadpole: Serra do Cipó – MG, Brazil (Eterovick & Sazima 1998).

Other characterizations: not available.

Specimens Examined: Brazil, Minas Gerais State, Parque Nacional de Sempre Vivas (ZUFG 931, ZUFG 937, ZUFG 984, ZUFG 991, ZUFG

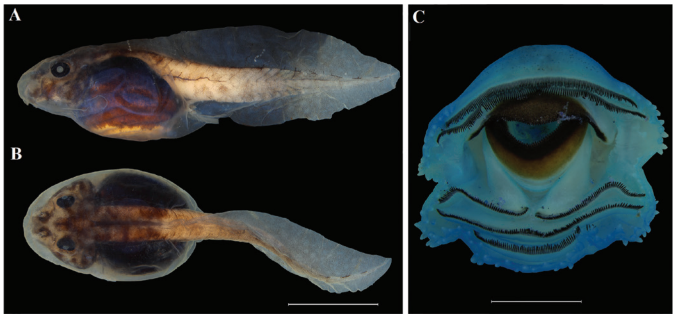

Figure 44. Tadpoles of *Odontophrynus* sp. at Stage 32 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

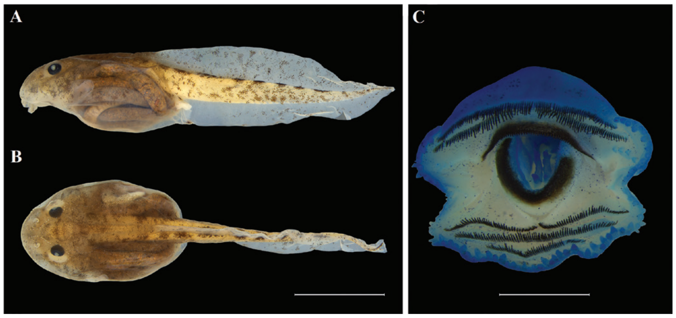

Figure 45. Tadpoles of *Proceratophrys boiei* at Stage 32 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

1007). Description based on 15 tadpoles between Gosner Stages 35 and 39.

Characterization. Total length 32.67 ± 4.61 mm (Table 1, Figure 46). The body shape is ovoid in dorsal view and globular-depressed in lateral view (BW/BH = 1.39–1.41). The snout is rounded in lateral view. The oral disc is ventral, laterally and lateroventrally emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae aggregated laterally, and smaller than the marginal papillae. LTRF is 2/3(1), A1 < A2, P1 = P2 > P3. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower. Nares medium (ND/ED = 0.15–0.21), elliptical, with a small projection on the marginal rim, dorsally positioned. Eyes medium (ED/BH = 0.21–0.24), dorsal positioned. Spiracle sinistral, short to medium (SL/BL = 0.05–0.13), narrow to medium (SW/BH = 0.05–0.11), opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to the body wall and free distal edge. Vent tube medial, fused to the ventral fin. The caudal musculature width is narrow to medium (TMW/BW = 0.25–0.31). The dorsal fin has medium height (DFH/TMH = 0.60–0.66) originating at the posterior third of the body with a median slope, with convex margin; ventral fin is low to medium (VFH/TMH = 0.36–0.70) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line not evident.

Comments. The tadpole presented in Eterovick & Sazima (1998) was described with the spiracle dorsally directed and without lateral emargination and folds on the lower labium. The tadpoles in our sample had lateral emargination and two folds in the lower labium, although not as prominent as seems in *P. boiei* and *P. dibernardoi*. The presence of lateral emargination and two folds in the lower labium were reported in tadpoles of *P. cururu* by Provete et al. (2013). Tadpoles of *P. cururu* differ from tadpoles of *P. boiei* by larger body proportions, less prominent folds in the lower labium and the greater number of submarginal papillae aggregated in the lateral of the oral disc, and the rounded tail tip.

Proceratophrys dibernardoi Brandão, Caramaschi, Vaz-Silva & Campos 2013

First Description of the tadpole: Jataí – GO, Brazil (Santos et al. 2017).

Other characterizations: not available.

Specimens Examined: Brazil, Goiás State, municipality of Jataí (ZUFG: 717).

Characterization. The following information is complementary to the description available in Santos et al. (2017). Total length 29.75 ± 1.52 mm (Table 1, Figure 47). The body shape is globular-depressed in lateral view (BW/BH = 1.46–1.52). Nares middle (ND/ED = 0.15–0.18) and eyes medium (ED/BH = 0.20–0.21). Spiracle short (SL/BL = 0.03–0.06) and narrow to medium width (SW/BH = 0.05–0.10). The caudal musculature width is medium (TMW/BW = 0.37–0.38), the dorsal fin has medium height (DFH/TMH = 0.53–0.54) and the ventral fin is low (DFH/TMH = 0.41–0.41).

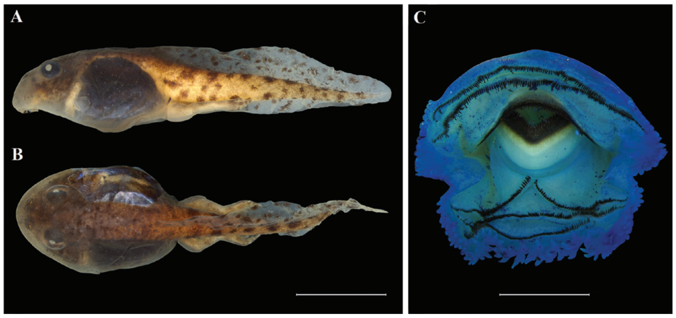

Figure 46. Tadpoles of *Proceratophrys cururu* at Stage 39 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

Comments. Santos et al. (2017) provided comparison with other species of the *P. cristiceps* group. Tadpoles of *P. dibernardoi* differ from tadpoles of *P. boiei* and *P. cururu* by the spiracle with centripetal wall completely fused to the body wall, lower body height, and wider marginal rim, especially when compared to *P. cururu*.

Proceratophrys salvatori Caramaschi 1996

First Description of the tadpole: Alto Paraíso – GO, Brazil (Brandão & Batista 2000).

Other characterizations: not available.

Specimens Examined: Brazil, Goiás, Parque Nacional da Chapada dos Veadeiros National (ZUFG 1886). Description based on six tadpoles between Gosner Stages 38 and 40.

Characterization. Total length 29.84 ± 1.91 mm (Table 1, Figure 48). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.15–1.18). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of elongated marginal papillae, interrupted by a dorsal gap; submarginal papillae absent. LTRF is 2(2)/3(1), A1 < A2, P1 = P2 > P3. The upper jaw sheath is wide, arc-shaped, and the lower jaw sheath is wide, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares medium (ND/ED = 0.17–0.20), rounded, with a small projection on the marginal

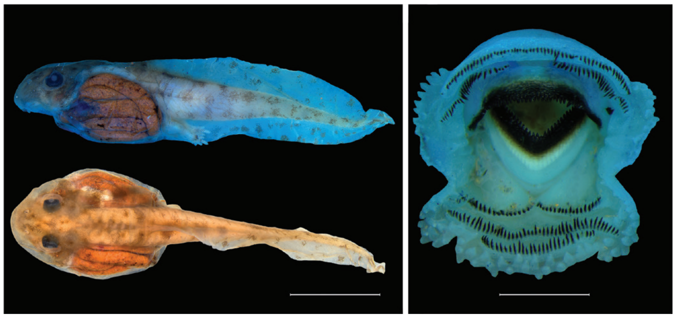

Figure 47. Tadpoles of *Proceratophrys dibernardoi* at Stage 37 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 30 (scale 2 mm).

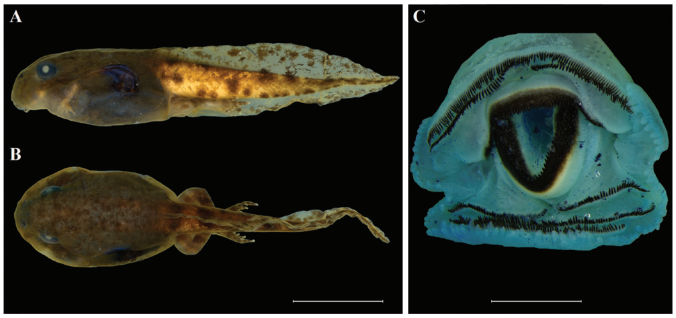

Figure 48. Tadpoles of *Proceratophrys salvatori* at Stage 40 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 39 (scale 2 mm).

rim, dorsally positioned. Eyes medium (ED/BH = 0.20–0.20), dorsally positioned. Spiracle sinistral, short to medium (SL/BL = 0.04–0.08), narrow to medium (SW/BH = 0.06–0.10), opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to body wall and free distal edge. Vent tube medial with dextral opening, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.30–0.33). The dorsal fin has medium height (DFH/TMH = 0.83–0.86), originating at the body-tail junction with an acute slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.44–0.49) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line not evident.

Comments. *Proceratophrys salvatori* was initially allocated in the genus *Odontophrynus*, and more recently transferred to the *Proceratophrys* genus (Magalhães et al. 2020). Tadpoles of *P. salvatori* can be distinguished from other *Proceratophrys* tadpoles included in our work by the nares with opening anterolaterally directed. Also, the pointed tail tip differentiates *Proceratophrys* cf. *goyana* from *P. cururu.*

Proceratophrys cf. *goyana*

First Description of the tadpole: not applicable.

Other characterizations: not available.

Specimens Examined: Brazil, Goiás State, municipality of Iporá (ZUFG 2269, ZUFG 2270, ZUFG 2271, ZUFG 2272, ZUFG 2273). Description based on ten tadpoles between Gosner Stages 31 and 37.

Characterization. Total length 35.56 ± 3.83 mm (Table 1, Figure 49). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.03–1.22). The snout is rounded in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae scattered laterally, with the same length of the marginal papillae. LTRF is 2(2)/3(1), A1 slightly smaller than A2, P1>P2>P3. The upper jaw sheath is narrow, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the lower jaw sheath is wider than the upper jaw sheath. Nares medium (ND/ED = 0.29–0.32), elliptical, with a projection on the marginal rim, dorsally positioned. Eyes medium (ED/BH = 0.19–0.19), dorsally positioned. Spiracle sinistral, short (SL/BL = 0.05–0.06), narrow (SW/BH = 0.07–0.09), with opening on the middle third of the body, posterodorsally directed, with the centripetal wall fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium to wide (TMW/BW = 0.44–0.49). The dorsal fin has medium height (DFH/TMH = 0.60–0.63), originating at the tail-body junction with acute slope, with convex margin; ventral fin is low (VFH/TMH = 0.42–0.42) with margin parallel to the caudal musculature; the tail tip is pointed. Lateral line not evident.

Comments. We are using the name *Proceratophrys* cf. *goyana* to these tadpoles once they were collected in the same pond were only adults of *P. goyana* were found and because a formal description of these tadpoles is lacking. The number of marginal papillae and the quantity and position of submarginal papillae presented variation among individuals in our sample. One individual has a uniseriate marginal papilla, two have submarginal papillae only laterally, two only ventrally, two does not have submarginal papillae and one have submarginal papillae larger than marginal papillae. Three individuals had the A2 teeth row slightly longer than the A1, and four individuals had the A1 with same size that the A2. Tadpoles of *Proceratophrys* cf. *goyana* can be distinguished from *P. boiei* by having larger body and the oral disc with only lateral emargination. Tadpoles of *Proceratophrys* cf. *goyana* differ from *P. dibernardoi* by the spiracle with a free distal margin, greater number of submarginal papillae, oral disc without folds ventrally in the lower labium, and dorsal fin originating on the the tail-body junction. Also, the absence of folds ventrally in the lower labium differentiate *Proceratophrys* cf. *goyana* from *P. cururu.*

Proceratophrys sp.

First Description of the tadpole: not applicable.

Other characterizations: not available.

Specimens Examined: Brazil, Goiás State, municipality of São Domingos (ZUFG 1043, ZUFG 1051). Description based on five tadpoles between Gosner Stages 31 and 39.

Characterization. Total length 27.55 ± 4.99 mm (Table 1, Figure 50). The body shape is elliptical in dorsal view and globular-depressed in lateral view (BW/BH = 1.22–1.24). The snout is sloped in lateral view. The oral disc is ventral, laterally emarginate, with a uniseriate row of conical marginal papillae, interrupted by a dorsal gap; submarginal papillae absent. LTRF is 2(2)/3(1), A1 slightly smaller than A2, P1 = P2 and P3 slightly smaller than P2. The upper jaw sheath is narrow to medium, arc-shaped, and the lower jaw sheath is narrow, U-shaped; the lower jaw sheath is wider than the upper jaw sheath. Nares very large (ND/ED = 0.81–0.89), elliptical, with a projection on the marginal rim, dorsolaterally positioned. Eyes small to medium (ED/BH = 0.16–0.19), dorsal positioned. Spiracle sinistral, with medium lenght (SL/BL = 0.13–0.14), medium to wide (SW/BH = 0.20–0.25), opening on the middle third of the body, posterodorsally directed, with the centripetal

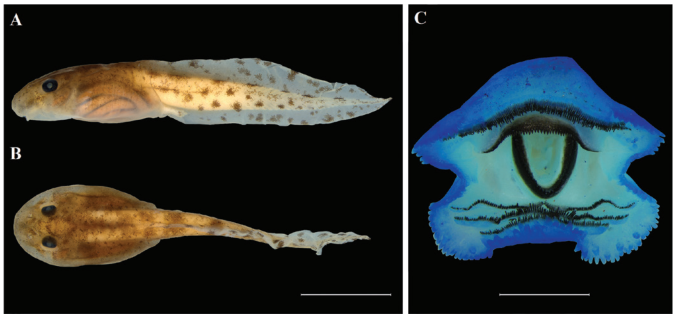

Figure 49. Tadpoles of a *Proceratophrys* cf. *goyana* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

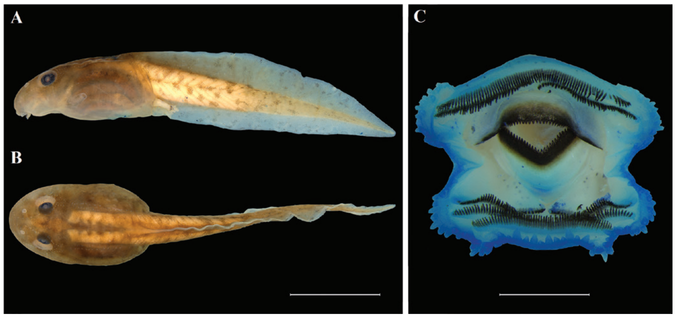

Figure 50. Tadpoles of a *Proceratophrys* sp. at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc at Stage 33 (scale 2 mm).

wall fused to body wall. Vent tube dextral, fused to the ventral fin. The caudal musculature width is medium (TMW/BW = 0.34–0.43). The dorsal fin has medium height (DFH/TMH = 0.68–0.81), originating at the body with median slope, and convex margin; ventral fin has medium height (VFH/TMH = 0.53–0.61) with margin parallel to the caudal musculature; the tail tip is rounded. Lateral line evident.

Comments. We were unable to associate this morphotype to the other known species of *Proceratophrys*. Tadpoles of *Proceratophrys* sp. differ from tadpoles of *P.* cf. *goyana*, *P. boiei* and *P. dibernardoi* by the sloped snout shape in lateral view and nares size. In addition, these tadpoles differ from *Proceratophrys* cf. *goyana* by the oral disc emarginate ventrally with two folds in the lower labium, and from *P. dibernardoi* by the spiracle with a free distal margin.

8. Phyllomedusidae Günther 1858

Pithecopus azureus Cope 1862

First Description of the tadpole: Argentina (Cei 1980).

Other characterizations: Populations from Salta and Formosa, Argentina, treated as *P. hypochondrialis*, had the oral disc described by Vera Candioti (2007); Bolívia (Schulze et al. 2015); Barro Alto, Cocalzinho, Mineiros and Jataí - GO, Brazil (Santos et al. 2018).

Specimens Examined: Brazil, Goiás State, municipalities of Barro Alto (ZUFG 819, ZUFG 838), Jataí (ZUFG 2350), Mineiros (ZUFG 746). Description based on 15 tadpoles between Gosner Stages 35 and 38.

Characterization. Total length 48.76 ± 4.97 mm (Table 1, Figure 51). The body shape is elliptical-elongated in dorsal view and triangular-compressed in lateral view (BW/BH = 0.83–0.92). The snout is truncated in lateral view. Oral disc anteroventral, ventrally emarginate, with a uniseriate row of elongated marginal papillae, in alternated disposition, interrupted by a dorsal gap; submarginal papillae scattered laterally, and smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 slightly smaller than A2, P1 = P2 and P3 with about a third of the P2 length. The upper jaw sheath is narrow to medium, M-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares small to medium (ND/ED = 0.08–0.21), elliptical, laterally positioned. Eyes medium (ED/BH = 0.26–0.30), laterally positioned. Spiracle ventral, short to medium (SL/BL = 0.06–0.09), with medium width (SW/BH = 0.13–0.16), opening at the middle third of the body, posteriorly directed, with the centripetal wall fused to the body wall. Vent tube medial with dextral opening, fused to the ventral fin. The caudal musculature width is wide (TMW/BW = 0.50–0.51). The dorsal fin is low (DFH/TMH = 0.28–0.43), originating at the tail-body junction with acute slope, with margin parallel to the caudal musculature; ventral fin has medium height (VFH/TMH = 0.57–0.73) with convex margin; the tail tip end with a flagellum. Lateral line evident.

Comments. Tadpoles described by Cei (1980) differed from the tadpoles in our sample by the LTRF 2(2)/2(1) and the dextral vent tube. The populations analyzed by Vera Candioti (2007) had uniseriate marginal papillae. Two morphotypes were presented by Schulze et al. (2015), from Bolivia, the "*P. azureus* A" and "*P. azureus* B" (treated as *Phyllomedusa azurea*). The morphotype B (Schulze et al. 2015) was described with a sloped snout in lateral view, arc-shaped upper jaw sheath, V-shaped lower jaw sheath, marginal papillae biseriate laterally and uniseriate in alternated disposition ventrally, and without submarginal papillae. The morphotype A (Schulze et al. 2015) also had a sloped snout in lateral view, but the marginal papillae were biseriate lateral and ventrally, and the submarginal papillae were absent. The morphotype A presented a narrow ventral gap, variation that we observed in seven tadpoles in our sample. Two individuals had ventral emargination in the oral disc, and one individual had a biseriate marginal papillae. The lateroventrally spiracle described by Schulze et al. (2015) represent a difference in terminology use, but the position is the same. We prefer the use of ventral spiracle, once the spiracle can be only seen in ventral position, although it is not positioned in the sagittal line.

Pithecopus oreades (Brandão, 2002)

First Description of the tadpole: Goiás – Brasil (Brandão, 2002).

Other characterizations: not available.

Specimens Examined: Brazil, Goiás State, Parque Nacional da Chapada dos Veadeiros (ZUFG 1976). Description based on eight tadpoles between Gosner Stages 36 and 38.

Characterization. Total length 48.72 ± 2.31 mm (Table 1, Figure 52). The body shape is elliptical-elongated in dorsal view and triangular-compressed in lateral view (BW/BH = 0.98–1.00). The snout is rounded to sloped in lateral view. The oral disc is anteroventral, ventrally emarginate, with a uniseriate row of elongated marginal papillae, in alternated disposition, interrupted by a dorsal and a small ventral gap; submarginal papillae scattered laterally, smaller than the marginal papillae. LTRF is 2(2)/3, A1 = A2, P1 = P2 > P3. The upper jaw sheath is narrow to medium, M-shaped, and the lower jaw sheath is narrow, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares medium (ND/ED = 0.23–0.26), elliptical, with a projection on the marginal rim, laterally positioned. Eyes medium (ED/BH =

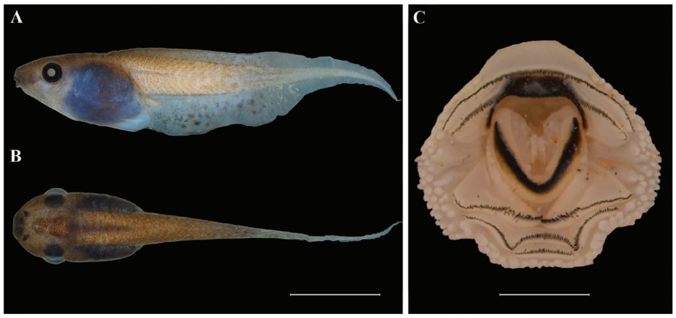

Figure 51. Tadpoles of *Pithecopus azureus* at Stage 35 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

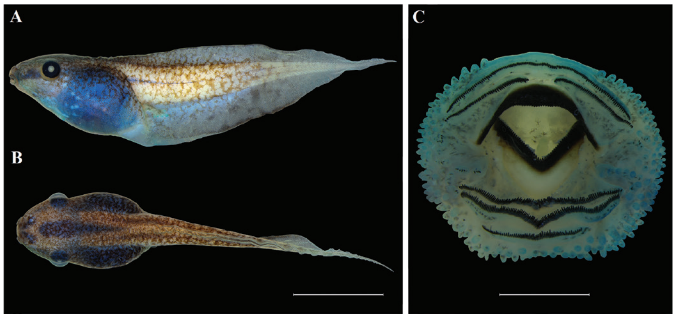

Figure 52. Tadpoles of *Pithecopus oreades* at Stage 36 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

0.25–0.26), laterally positioned. Spiracle ventral, short to medium (SL/BL = 0.05–0.09), with medium width (SW/BH = 0.11–0.15), opening at the middle third of the body, posteriorly directed, displaced to the left, with the centripetal wall fused to the body wall. Vent tube medial with dextral opening, fused to the ventral fin. The caudal musculature width is medium to wide (TMW/BW = 0.45–0.51). The dorsal fin is low (DFW/TMW = 0.39–0.40), originating at the tail-body junction with acute slope, with margin parallel to the caudal musculature; ventral fin has medium height (VFH/TMH = 0.57–0.70) with convex margin; the tail end with a flagellum. Lateral line evident.

Comments. Our tadpoles are like those described by Brandão (2002), but the presence of a narrow ventral gap was not reported in the original description. Tadpoles of *P. oreades* can be distinguished from tadpoles of *P. azurea* by the P3 teeth row slightly smaller than P2 and P1, labial teeth row formula 2(2)/3, and spiracle opening oriented to the left.

Pithecopus sp.

First Description of the tadpole: not applicable.

Other characterizations: not available.

Specimens Examined: Brazil, Goiás State, municipality of Pontalina (ZUFG 1294). Description based on two tadpoles at Gosner Stage 34.

Characterization. Total length 42.10 ± 0.79 mm (Table 1, Figure 53). The body shape is elliptical-elongated in dorsal view and triangular-compressed in lateral view (BW/BH = 0.82–0.94). The snout is truncated in lateral view. The oral disc is anteroventral, ventrally emarginate, with a uniseriate row of elongated marginal papillae, in alternated disposition, interrupted by a dorsal gap; submarginal papillae scattered laterally, smaller than the marginal papillae. LTRF is 2(2)/3(1), A1 = A2, P1 > P2 > P3. The upper jaw sheath is narrow to medium, M-shaped, and the lower jaw is narrow, V-shaped; the upper jaw sheath is wider than the lower jaw sheath. Nares small (ND/ED = 0.08–0.08), elliptical, with a projection on the marginal rim, laterally positioned. Eyes large (ED/BH = 0.32–0.32), laterally positioned. Spiracle ventral, short (SL/BL = 0.05–0.06), with medium width (SW/BH = 0.12–0.14), opening at the middle third of the body, posteriorly directed, with centripetal wall fused to the body wall. Vent tube medial with dextral opening, fused to the ventral fin. The caudal musculature width is wide (TMW/BW = 0.56–0.60). The dorsal fin is low (DFH/TMH = 0.21–0.23), originating at the tail-body junction with acute slope, with margin parallel to the caudal musculature; ventral fin is low (VFH/TMH = 0.40–0.41) with convex margin. Lateral line evident.

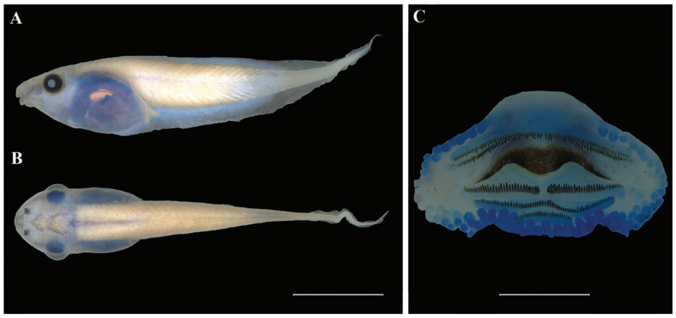

Figure 53. Tadpoles of *Pithecopus* sp. at Stage 34 (Gosner 1960): (A) lateral, and (B) dorsal view (scale 10 mm), (C) oral disc (scale 2 mm).

Comments. We were unable to associate this morphotype to the other known species of *Pithecopus*. Tadpoles of *Pithecopus* sp. differ from tadpoles of *P. azurea* and *P. oreades* by the taller caudal musculature, lower dorsal fin, and smaller total length. In one individual, we observed a narrow ventral gap.

Discussion

Most larval studies in Brazil are related to descriptive studies, like the description of the external morphology (Andrade *et al.* 2007), which allow the inclusion of larval morphology as functional or ecological traits in hypothesis test (e.g., Arifin et al. 2021). However, we still need to understand the extent of variation in morphological traits to increase the accuracy of taxonomic studies, and its usefulness in ecological studies. In the characterizations that we provided in this article, we found variation in the body or oral features even for species that we do not have a larger sample, which highlight the need to not underestimate the amount of intra- or interpopulation morphological variation and the impact of such variation in defining morphotypes for taxonomic studies (Grosjean 2005) or evaluating the effect of environmental modifications (e.g., Costa & Nomura 2016, Costa et al. 2017), for example. Moreover, tadpoles are known to exhibit phenotypic plasticity and morphological variation in tadpoles is expected throughout its area of occurrence, due to changes in local environmental conditions or the presence of predators and competitors (Marques & Nomura 2018). In general, morphological characterization of the external morphology of tadpoles does not receive much attention from researchers or journals, with several journals indicating that tadpole morphological characterization should be published as Short Notes or Correspondence (e.g., Santos et al. 2018, Tolledo & Toledo 2010, Verdade et al. 2023). Certainly, we can have many arguments for a given report to be published as a summarized version, but this decision ideally should be done case by case, once this type of publication reduces the opportunity for discussion of the results and for comparisons. Also, when a given tadpole morphology is already formally described, the interest to report other characterization of the same tadpole with samples from different localities is reduced, unless the original description is not very detailed, have a low sample of individuals, or is based on individuals in early developmental stages (i.e., below Gosner's Stage 34). Such constraint in reporting morphological variation, despite its result from the interest of researchers for novelty or journal editorial decisions, implies a generalization of the tadpole morphology based on the first description for the entire range of the species distribution and restricts the morphological sampling throughout the geographical range of the species. Although the effect of availability is not restricted to the reports of tadpoles' morphology, it is an issue to be considered, nevertheless. One of the possibilities to overcome this effect is to produce descriptive reports with broader geographical samples and to use more diverse and comparative analytical methods. However, in a continental size country like Brazil, this sampling and analytical decisions can result in greater logistical costs, which could be prohibitive, once financial resource is an important constraint of biodiversity research in developing countries (Young 2005). The increase of independent and geographically restricted reports of tadpoles' morphology would help to reduce several opportunities costs and increase the open collaboration in biodiversity research, aligned to the principles and practices of the open science initiative (UNESCO 2021).

The ontogenetic variation can lead to erroneous determination of diagnostic traits (see Gosner 1960, Grosjean 2005, and Navarro Acosta & Vera Candioti 2017 for a discussion about morphological variation regarding developmental allometry). To avoid this problem, the use of tadpoles between Stages 32 and 40 was suggested by Grosjean (2005), once it is more likely that any variation in these developmental stages reflect interspecific variation than ontogenetic changes. It would be ideal if all anuran species had a known developmental table for the larval stage, but we are far from this reality. Even if we consider that the ontogenetic changes in the larval stage among anuran species is relatively uniform, and then could be illustrated by the Gosner's (1960) developmental table, we do not have enough information about populational variation to define which are the most reliable traits for taxonomic comparisons.

The shape of the snout, the body or fins or the size of eyes and nares had great variation in tadpoles' descriptions. The use of morphological traits as nominal variables increases the risk of subjective interpretation of such traits. Although the variability in the reports of the external morphology could represent a natural variation in a continuous shape scale, and the use of nominal descriptors in the characterization is also useful to describe tadpole morphology, the use of quantitative morphometric definitions for such shapes would increase reliability in tadpoles' descriptions. An attempt to provide morphological definitions was made by Altig (1970), modified posteriorly by Altig & McDiarmind (1986, 1999). Despite being widely used, in many descriptions several traits are lacking, or the traits are not used as proposed. Together with the terminology problem, the use of ratios to describe tadpole morphology limits the utility of the descriptions. Although ratios are helpful to establish a size proportion of the morphological trait, we cannot access the raw information from ratios. Conversely, the use of new technologies in image capture and processing allowed an increase in the quality of pictures in recent descriptions of tadpoles' external morphology (e.g., *Chiasmocleis schubarti*, Santos et al. 2015; *Crossodactylus aeneus*, Silva-Soares et al. 2015; *Dendropsophus branneri*, Abreu et al. 2015), and the use of quantitative morphometric analytical approaches, as geometric morphometric (e.g., Pezzuti et al. 2016).

We detected large variation in external morphological traits of tadpoles from several anuran species, with no reference in other available descriptions of such variation. Evaluation if these variations represent some level of phenotypic plasticity or a clue for taxonomic use, like a complex of cryptic species, is hard to define once data about morphological traits from populations throughout a geographic gradient is lacking.

1. How to use this taxonomic key

We think this taxonomic key would be helpful to anyone interested in describing the anuran biodiversity using larval stage information, but the users should be aware of its limitations. First, the distribution of anuran species in the Cerrado Biome is compartmentalized, thus many species that occur in the Cerrado-Atlantic Forest border are not expected to be found in the Cerrado-Amazon border, and vice-versa (Valdujo et al. 2012). The user should know the expected species pool for the sampled area to avoid misidentification. Second, we should expect variation in tadpole morphology; thus, the user should compare the tadpole morphology with the larval description before associating a larval morphology with a species name. This taxonomic key includes about 22% of the species known to occur in the Cerrado biome, and for many anurans' species larval stage is currently unknown. For example, for the 114 anurans species that occur in the Goiás State, central Brazil, 35 does not have their larval stage described (Vaz-Silva et al. 2020). Thus, the user should be aware that this taxonomic key can be useful to indicate which species the larva belongs to or exclude other species to which the larva does not belong. Finally, we invite other researchers with samples of tadpoles' larvae of species not included to modify this taxonomic key to improve its accuracy and species coverage.

Identification key

1. Nares unperforated 2

 1'. Nares perforated 4

2. Double dermal flap covering the mouth, vent tube with sinistral opening .... *Elachistocleis cesarii*

 2'. A single continuous dermal flap covering the mouth, vent tube with medial opening 3

3. Total length above 30 mm in stage 37, snout rounded in lateral view, dorsal fin originating at the body-tail junction …............................ ....*Dermatonotus muelleri*

 3'. Total length below 25 mm in stage 37, snout truncate in lateral view, dorsal fin originating at the posterior third of the body ………………................................. *Chiasmocleis albopunctata*

4. Accessory teeth row present laterally in the oral disc ..…………… 5

 4'. Accessory teeth row absent laterally in the oral disc …..…….…. 8

5. Small anterior gap in the marginal papillae, snout rounded in lateral view, nares with projection on the marginal rim …………………….. 6

 5'. Wide anterior gap in the marginal papillae, snout sloped in lateral view, nares without projection on the marginal rim ………….. …..……. *Trachycephalus typhonius*

6. Spiracle with the centripetal wall fused to body wall and free distal edge, vent tube short 7

 6'. Spiracle with centripetal wall not fused to the body wall and longer than external wall, vent tube long …....... *Boana lundii*

7. Presence of dark rounded blotches scattered on the dorsum of the body, two labial teeth row anterior, labial teeth row formula (LTRF) 2(2)/5(1) .... *Bokermannohyla sapiranga*

 7'. Absence of dark rounded blotches scattered on the dorsum of the body, three labial teeth row anterior, LTRF 3(1,3)/6(1) ……….....…………………… *Bokermannohyla pseudopseudis*

8. Dorsal and ventral fins margin parallel to the caudal musculature …. 9

 8'. Dorsal and ventral fins not as above ……………………….... 13

9. Oral disc not emarginated ………...…………………………... 10

 9'. Oral disc emarginated ……………………………….....… 11

10. Oral disc anteroventral, snout rounded in lateral view, marginal papillae short and rounded, labial teeth row 1/2(1), total length 58.72 mm ……….......…………..... *Leptodactylus labyrinthicus*

 10'. Oral disc ventral, snout sloped in lateral view, marginal papillae elongated, labial teeth row 2(2)/3, total length 35.77 mm ………..................................……… *Leptodactylus troglodytes*

11. Body rounded in dorsal view, globular in lateral view, oral disc anteroventral, laterally emarginated, papillae absent at the emargination …................................ *Adelphobates galactonotus*

    11’. Body in dorsal view globular or elliptic, depressed in lateral view, oral disc ventral, ventrally emarginate, papillae present at the emargination ………...................…………………...... 12

12. Body ovoid in dorsal view, nares anterodorsally directed, dorsal fin originating at the middle third of the tail ...... *Thoropa megatympanum*

    12’. Body elliptical in dorsal view, nares dorsolaterally directed, dorsal fin originating at the posterior third the tail ……………………...…………………...…. *Thoropa miliaris*

13. Spiracle ventral 14

    13’. Spiracle sinistral …………………...……………........….. 16

14. Labial teeth row 2(2)/3, spiracle displaced to the left side of the belly …………………………………………. *Pithecopus oreades*

    14’. Labial teeth row 2(2)/3(1), spiracle positioned near the sagittal line ....……… 15

15. Nares with a projection on the marginal rim, total length with average of 42.10 mm and ventral fin with about 1.09 mm ………………. ..…...…………………... *Pithecopus* sp.

    15’. Nares without a projection on the marginal rim, total length with average of 48.76 mm and ventral fin with about 1.44 mm …………………….................…….... *Pithecopus azureus*

16. Body rounded in dorsal view, nares rounded, oral discs not emarginated, with posterior margin concave when closed …........17

    16’. Body not rounded, nares elliptical or reniform, oral disc emarginated, not forming a concave shape when closed …......18

17. Large oral disc, without dorsal gap, submarginal papillae aggregated lateroventrally, T-shaped papillae present, upper jaw sheat arc-shaped …...……..….…. *Scinax pombali*

    17’. Smaller oral disc with dorsal gap, submarginal papillae aggregated laterally, T-shaped papillae absent, upper jaw sheath M-shaped …….....................……………... *Scinax longilineus*

18. Upper labial teeth rows absent or with only one row ……..….... 19

    18’. Two or more upper labial teeth rows ………….……..….... 20

19. Oral disc interrupted by lateroventral gaps, margin of fins convex, upper jaw sheath U-Shaped ...……………. *Dendropsophus soaresi*

    19’. Oral disc not interrupted by lateroventral gaps, fins high and triangular, upper jaw sheath arc-shaped …………….. ....… *Dendropsophus minutus*

20. Eyes dorsal, body globular in lateral view ………........……… 21

    20’. Eyes lateral, body triangular in lateral view ……….……. 45

21. Marginal papillae interrupted by ventral gap ……………....…… 22

    21’. Marginal papillae not interrupted by ventral gap …………… 28

22. Oral disc with two rows of posterior labial teeth ……....……... 23

    22’. Oral disc with three rows of posterior teeth …………… 24

23. Spiracle positioned bellow the body midline in lateral view, ventrally directed, nares medium, absence of a medial gap in P1 ...………........……..................………… *Physalaemus centralis*

    23’. Spiracle positioned at the body midline in lateral view, posterodorsally directed, nares large to very large, presence of a medial gap in P1……............ *Physalaemus marmoratus*

24. P3 longer than half the length of the P2, nares medium to large ……………...…..... 25

    24’. P3 shorter than one third the length of the P2, nares very large ……......................................………... *Physalaemus cuvieri*

25. Rounded tail tip, caudal musculature not reaching the tail tip, spiracle with centripetal wall longer than the external wall, wide ventral gap ……………………………………………...…. 26

    25’. Pointed tail tip, caudal musculature almost reaching the tail tip, spiracle with centripetal wall with the same length of the external wall, without ventral gap ………...…..... *Physalaemus nattereri*

26. Unpigmented longitudinal stripe along the ventral edge of the tail musculature …... 27

    26’. Unpigmented longitudinal stripe along the ventral edge of the tail musculature absent …………………. *Rhinella cerradensis*

27. Spiracle opening on the midbody, eyes laterally directed ……. ....….. *Rhinella diptycha*

    27’. Spiracle opening on the posterior third of the body, eyes dorsolaterally directed ……….... *Rhinella crucifer* x *R. ornata*

28. Nares large, with a large projection on marginal rim, spiracle long, centripetal wall not fused to body wall and with the same length of the external wall …...…...…...…… 29

    28’. Nares small, without projection on marginal rim, spiracle short, centripetal wall fused to the body wall and longer than the external wall ……………...….................………….... 30

29. Marginal papillae triangular, submarginal papillae present, dorsal fin triangular …………………..………………. *Boana raniceps*

    29’. Marginal papillae conical, submarginal papillae absent, dorsal fin convex ………………………… *Boana albopunctata*

30. Oral disc not emarginate ……….……………………………... 31

    30’. Oral disc emarginate ……………....………………………… 34

31. Vent tube long, medial, upper jaw sheath arc-shaped, submarginal papillae absent ……………...………………………………… 32

    31’. Vent tube short, dextral, upper jaw sheath M-shaped, submarginal papillae shorter, laterally aggregate on the oral disc ……...……………………….........…… *Scinax rupestris*

32. Total length below 40 mm, marginal papillae not biseriate ventrally and not triseriate laterally, spiracle at the midline of the body at lateral view, pointed tail tip ……………......................................… 33

    32’. Total length above 45 mm, marginal papillae biseriate ventrally and triseriate laterally, spiracle bellow the midline of the body at lateral view, rounded tail tip …………… *Leptodactylus latrans*

33. A2 teeth row without a medial gap, marginal papillae biseriate ventrally, snout rounded in lateral view ………….. …...……….................……………….. *Leptodactylus podicipinus*

    33’. A2 teeth row with a medial gap, marginal papillae uniseriate in alternate disposition, snout sloped in lateral view ……….. ……..… *Leptodactylus fuscus*

34. Oral disc emarginate ventrally ………....................................…... 35

34’. Oral disc emarginate laterally ………...…...…...…..........……... 36

35. Body elliptical in dorsal view, nares without projection on the marginal rim, five posterior rows of labial teeth …………………... .... *Bokermannohyla alvarengai*

35’. Body ovoid in dorsal view, nares with a large projection on the marginal rim, four posterior rows of labial teeth …………………………...…….........…... *Boana* cf. *crepitans*

36. Intestinal tube switchback point located at to the center of abdominal region …... 37

36’. Intestinal tube switchback point located at to the left of abdominal region ……………………... *Ameerega flavopicta*

37. Rounded tail tip 38

37’. Pointed tail tip 41

38. Total length less than 50 mm, upper jaw sheath arc-shaped, submarginal papillae present ……….......……..……………... 39

38’. Total length above 50 mm, upper jaw sheath M-shaped, submarginal papillae absent ……….....…. *Odontophrynus* sp.

39. Presence of medial gap in the A2 teeth row …….......………... 40

39’. Labial teeth row A2 not interrupted …… *Proceratophrys cururu*

40. Body elliptical in dorsal view, depressed in lateral view, maximum total length of 38 mm and lower dorsal fin ………………. .... *Odontophrynus cultripes*

40’. Body ovoid in dorsal view, globular in lateral view, maximum total length of 48 mm and higher dorsal fin …...…. ………...…........………… *Odontophrynus* sp. (cf. *juquinha*)

41. Nares closer to snout tip than eyes, directed anterolaterally, large gap in P1 teeth row .... *Proceratophrys salvatori*

41’. Nares at equal distance from eyes and snout tip, not directed anterolaterally, small gap in P1 teeth row 42

42. Spiracle conspicuous, with centripetal wall not fused to the body wall, or with the distal margin free 43

42’. Spiracle inconspicuous, with centripetal wall completely fused to the body wall ……...……… *Proceratophrys dibernardoi*

43. Spiracle positioned below body midline ……….........……... 44

43’. Spiracle positioned above body midline ....… *Proceratophrys boiei*

44. Nares medium, folds on the lower labium absent, spiracle short .... *Proceratophrys* cf. *goyana*

44’. Nares very large, two folds on the lower labium, spiracle medium .... *Proceratophrys* sp.

45. Posterior third of the tail not pigmented …...…………...….… 46

45’. Posterior third of the tail heavily pigmented ………......... ....…. *Scinax squalirostris*

46. Dorsal fin emerging closer to the eye ……………….........….. 47

46’. Dorsal fin emerging posteriorly to the eye ……………….... 48

47. Snout rounded in lateral view, eyes large, jaw sheaths narrow .... *Scinax fuscomarginatus*

47’. Snout sloped in lateral view, eyes medium, jaw sheaths wide .... *Scinax fuscovarius*

48. Spiracle conspicuous, nares with opening directed laterally, upper jaw sheath arc-shaped ……………...……………... *Scinax* gr. *ruber*

48’. Spiracle inconspicuous, nares with opening directed anterolaterally, upper jaw sheath M-shaped …... *Scinax similis*

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Authors Contributions

Danusy Lopes Santos: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analyses and interpretation; contribution to manuscript preparation; contribution to critical revision; adding intellectual content.

Renato Neves Feio: Contribution to data collection; contribution to data analyses and interpretation; contribution to critical revision; adding intellectual content.

Fausto Nomura: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analyses and interpretation; contribution to manuscript preparation; contribution to critical revision; adding intellectual content.

Conflict of Interests

The authors declares that they have no conflict of interest related to the publication of this manuscript.

Data Availability

The morphometric raw data can be accessed at https://doi.org/10.48331/scielodata.HI0HTL

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Short Communication

Hidden in the dung: first record of *Maculantrops hirtipes* (Macquart, 1844) (Diptera, Sphaeroceridae) from Brazil

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***Abstract*:** We recorded for the first time the lesser dung fly *Maculantrops hirtipes* (Macquart, 1844) from Brazil, state of Rio Grande do Sul. Twenty-five specimens were reared from the dung of *Myocastor coypus* (Molina, 1782), this is the first record of the feeding substrate for the genus *Maculantrops* and the second only for the Archiborborinae. In addition, we describe the puparium, provide an updated distribution map and additional photographs of the species.

Keywords: *Sphaeroceridae; small dung flies; Neotropical region; new records.*

Escondido no esterco: primeiro registro de *Maculantrops hirtipes* (Macquart, 1844) (Diptera, Sphaeroceridae) do Brasil

Resumo: Registramos pela primeira vez a mosca-do-esterco *Maculantrops hirtipes* (Macquart, 1844) no Brasil, no estado do Rio Grande do Sul. Vinte e cinco espécimes foram obtidos em amostras fecais de *Myocastor coypus* (Molina, 1782). Este é o primeiro registro do substrato alimentar para o gênero *Maculantrops* e o segundo apenas para subfamília Archiborborinae. Além disso, descrevemos o pupário, fornecemos um mapa de distribuição atualizado e fotografias adicionais da espécie.

Palavras-chave: *Sphaeroceridae; mosca-pequena-do-esterco; região Neotropical; novos registros.*

Introduction

Lesser dung flies (Diptera, Sphaeroceridae) are a small, worldwide distributed Acalyptratae family composed of 59 genera and over 1800 species (Papp & Roháček 2021). Species of sphaerocerid feed as larvae on a wide variety of decaying organic matter including dung, rotting vegetation, and fungi. The family is easily recognized by the short, broad hind basitarsus. The Archiborborinae is an exclusively Neotropical subfamily containing 117 described species in 8 genera (Kits & Marshall 2013, Kits & Marshall 2015). Only one of these species, *Antrops truncipennis* (Enderlein, 1909), has had the immature stages and their biology described (Harrison 1970, Chown 1996 a, b).

The genus *Maculantrops* was erected by Kits & Marshall (2013) on the split of the wide paraphyletic genus *Archiborborus* (Duda, 1921) and comprises two valid species: *M. altiplanus* Kits & Marshall, 2013 (highlands of Bolivia) and *M. hirtipes* (Macquart, 1844) (widespread in Argentina, Chile and Uruguay).

The nutria *Myocastor coypus* (Molina, 1782) is a Neotropical semiaquatic species that has herbivorous habits, distributed from Bolivia to southern Argentina and Chile (Woods et al. 1992, Colares et al. 2010, IUCN 2016). In Brazil, the species has its native distribution restricted to the southern, from the state of Paraná to the state of Rio Grande do Sul (Moojen 1952, Cherem et al. 2004, IUCN 2016, Peixoto-Couto et al. 2022). However, there are records of the species in the states of Rio de Janeiro (Bueno 2013), Mato Grosso do Sul (Peixoto-Couto et al. 2022), and an introduction in São Paulo (De Vivo et al. 2011). Due to its high potential to colonize available habitats (Bueno 2013), it may also occur in other states. They are large rodents, ranging between 40 cm and 60 cm long, weighing between 5 and 9 kg (Waterkeyn et al. 2010). Much of its diet is composed of aquatic plants of different species, the Poaceae family being the most common (Colares et al. 2010). They live associated with bodies of water, preferably where the terrain offers ravines or walls where they dig their refuge burrows

(Silva 2014). In wetlands characterized by large expanses of water, they build their refuges on vegetation with pieces of reeds and grass, which can form large platforms (Silva 2014). The presence of trails, excavations, as well as the cylindrical, elongated and green feces are indications of the presence of this rodent (Silva 2014).

The Brazilian sphaerocerid fauna is poorly studied, with only 82 species in 28 genera registered (Miranda 2023), but this number does not reflect the real diversity of the family in the country. In this paper, we present the first report of *M. hirtipes* in Brazil. Additionally, we describe the puparium and the substrate on which the flies developed. We also provide an updated distribution map and include additional photographs of the species.

Material and Methods

Forty-two dung samples (Figure 1C, D, E) of *M. coypus* were collected at the Taim Ecological Station "32°37'33.93S 52°34'41.02W" state of Rio Grande do Sul, Brazil (Figure 1A, B) in August (rainy season) of 2022 and stored in 50 ml tubes and taken to the laboratory of Universidade do Vale do Rio dos Sinos. The samples were kept in the refrigerator at ±4°C for 27 days, when the first author noticed that there were flies walking inside the tubes. The flies were identified as Archiborborinae using the identification key to the genera of Sphaeroceridae of the Neotropical Region and Nearctic Mexico (Marshall & Buck 2010) and later as *Maculantrops hirtipes* using the work of Kits & Marshall (2013). The individuals were euthanized 24 hours after emergence, using cotton soaked with ethyl acetate, then pinned, labeled and deposited at the zoological collection of Unisinos. The species distribution map was created with QGIS 3.18 using coordinates from the specimen labels and locality data published in Kits & Marshall (2013) and (IUCN 2016).

The Taim Ecological Station (ESEC Taim) is a federal conservation unit located in the extreme south of Brazil. Created in 1986 on the borders of the municipalities of Rio Grande and Santa Vitória do Palmar in the state of Rio Grande do Sul, ESEC Taim protects vast wetlands, lakes, fields, dunes, forests and beaches (ICMBio 2021). It is considered one of the places with the greatest ecological significance in southern Brazil, as it provides shelter, food and a breeding ground for many species (ICMBio 2021). It is a priority area with extremely high importance for the preservation of the Pampa biome (MMA 2007).

The Taim wetlands have international relevance, protect several endemic species and have been recognized since 2017 as a RAMSAR site (ICMBio 2021). The annual average minimum temperature comprises around 23 and 14 ºC in summer and winter (Wrege et al. 2012) and the annual pluviometric precipitation varies between 1440 mm and 1452 mm (Simiioni & Wollmann 2016). Relative air humidity is 80% and remains high throughout the year (Tucci et al. 1996).

Results

Maculantrops hirtipes **(Macquart, 1844)** (Figures 2–3)

Borborus hirtipes Macquart, 1844: 424 Type locality: Chile.

Diagnosis. Easily recognized by the numerous dark spots on the wing and pattern of bands on the legs (Fig. 2A, B) (See Kits & Marshall (2013) for a complete description).

Figure 1. A–C. Living habitat and collection site of dung of *Myocastor coypus* (Molina, 1782). A. Drainage canal parallel to BR-471 highway, In the left one cattle individual and a group of six capybaras; B. Group of five *M. coypus* grazing together with a Southern screamer *Chauna torquata* (Oken, 1816) large bird on the right and a Southern lapwing *Vanellus chilensis* (Molina, 1782) on the lower right corner; C. Dung sample of *M. coypus*. D-E. Tubes with samples with dung stirred and whole respectively.

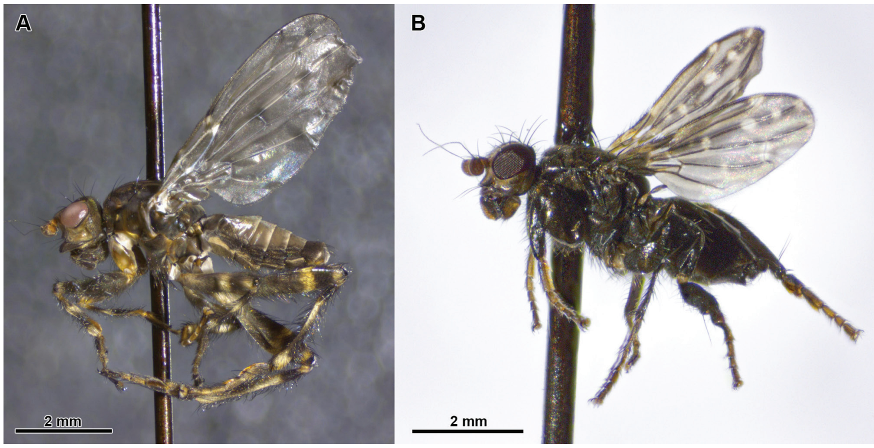

Figure 2. Habitus in lateral view of *Maculantrops hirtipes* (Macquart, 1844). A. Male; B. Female.

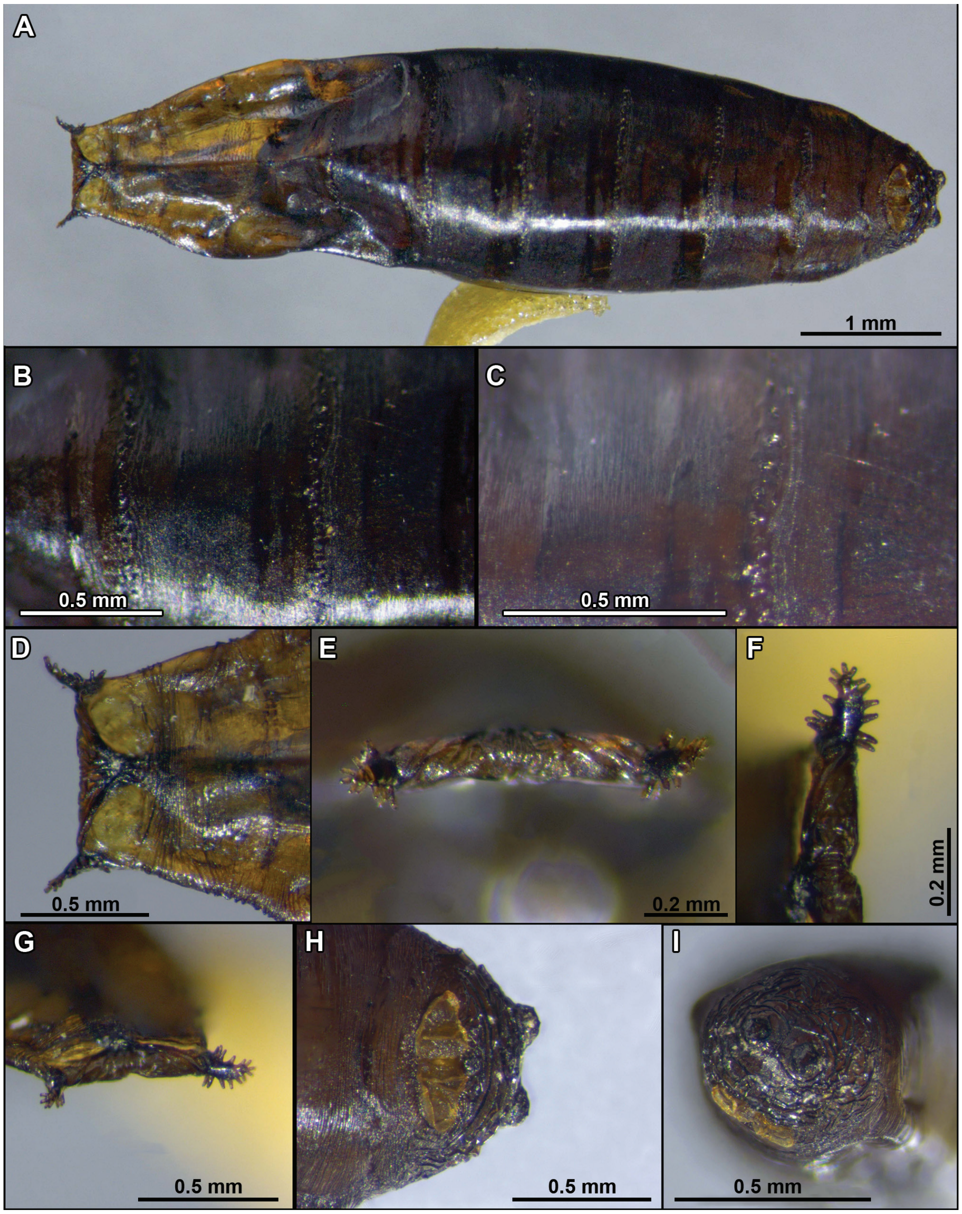

Figure 3. Puparium of *Maculantrops hirtipes* (Macquart, 1844). A. Habitus, ventral view; B-C. Creeping welts, ventral view; D–G. Anterior spiracular processes in ventral, anterior, lateral and anterolateral views respectively; H. Anal segment with reticulate wrinkling. I. Posterior spiracular processes, posterior view.

Figure 4. Known geographic distribution of *Maculantrops hirtipes* (Macquart, 1844) and native distribution of *Myocastor coypus* (Molina, 1782) according IUCN 2016.

Description of puparium (Figure 3). Pupa length: 6.3–7.2 mm. Color yellowish to dark brown, wrinkled transversely (Figure 3A). Abdomen with creeping welts present on anteroventral margin of segments 1–8 (Figure 3A–C). Welts consisting of widely separated, rounded teeth, those on segments 2–8 additionally with 2–3 irregular rows of minute teeth posterior to the larger teeth (Figure 3B, C). Anterior spiracular processes about twice their basal width, each bearing about 12–14 irregularly arranged papillae in a fan shape (Figure 3D–G). Anal segment with reticulate wrinkling (Figure 3H), posterior spiracular processes elevated about half their basal width, spiracular plates without hairs (Figure 3I).

Examined material: BRAZIL, Rio Grande do Sul, ESEC Taim, 32°37'33.93"S 52°34'41.02"W. *M. coypus* dung samples were collected from 26 to 28 August 2022 by P.H.O. Hoffmann & A. Adolfo. The first observation of adult flies in the samples was made on 23 September 2022 by P.H.O. Hoffmann.

Distribution. Argentina, Brazil (State of Rio Grande do Sul, new country record), Chile and Uruguay (Figure 4).

Discussion

Of the 45 fecal samples of *M. coypus* analyzed (Figure 1C), four showed hatching flies, representing a percentage of occurrence of 9%. A total of 25 adult specimens, 23 females, two males and 22 pupae of *M. hirtipes* were recovered from the samples. The samples with larvae of *Maculantrops* are easily recognized by the dung stirred up by the tube (Figure 1D) in contrast to the tubes without larvae where the dung remains whole (Figure 1E).

The *Myocastor coypus* (Figure 1A, B) has its diet based on aquatic plants, feeding mainly on plants from the Poaceae family (Colares et al. 2010). Can feed on 26 different plants, but species such as *Panicum tricholaenoides* Steud. and *Paspalum disthichum* L. are among the most frequent in the diet of this rodent in the study region (Colares et al. 2010). As the nutria, the capybara *Hydrochoerus hydrochaeris* (Linnaeus, 1766) has its diet based on aquatic plants, as well as the nutria of the Poaceae family is more common (Borges & Colares 2007). The capybara is the biggest rodent species of the world (Mones & Ojasti 1986) and occurs in sympatry with nutria in the study area. During the sampling fields we also collected 50 capybara dung samples. But despite going through the same storage methodology and having similarities in their diet, no flies were observed in capybara samples.

The known distribution of *M. hirtipes* shows remarkable overlap with the native distribution of *M. coypus*. Therefore, the distribution of *M. hirtipes* may be wider, reaching Paraguay and Bolivia, and the states of Santa Catarina and Paraná in southern Brazil. This pattern of co-distribution, along with the apparent absence of *M. hirtipes* in dung of *H. hydrochaeris*, may indicate specialization on the dung of this species. Sampling and rearing from mammal dung elsewhere in the range would be needed to more thoroughly address this.

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Leonardo Maltchik: Resources; Writing – review & editing.

Conflicts of Interest

The author(s) declare(s) that they have no conflict of interest related to the publication of this manuscript.

Data Availability

Supporting data are available at < https://www.scielo.br/journal/bn/about/#instructions>.

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Short Communication

New records of Ceratocampinae (Lepidoptera: Saturniidae) species from the Cerrado of Maranhão, Brazil

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Abstract: Ceratocampinae (Lepidoptera: Saturniidae) is the second most diverse subfamily of Saturniidae with 300 species described in 30 genera from southern Canada to northern Argentina. Species of this subfamily are widely distributed in Southeast Brazil, with many endemics to the Cerrado, and important as indicators of ecosystem quality. Specimens of Ceratocampinae were collected in the Parque Estadual do Mirador, Maranhão state, Brazil. *Adeloneivaia acuta* (Schaus, 1896), *Adeloneivaia schubarti* Barros & O. Mielke, 1970, *Eacles penelope* (Cramer, 1775) and *Megaceresa pulchra* (Bouvier, 1923) are recorded for the first time in Maranhão state and Northeast Brazil and *Eacles fairchildi* May & Oiticica, 1941, only for Maranhão. The record of five Ceratocampinae (Saturniidae) species increases the knowledge on the diversity and the importance of preserving those of this subfamily in the Cerrado biome of Maranhão state and the Northeast region of Brazil.

Keywords: *Conservation; Diversity; Moths; Northeast Brazil.*

Novos registros de espécies de Ceratocampinae (Lepidoptera: Saturniidae) para o Cerrado do Maranhão, Brasil

Resumo: Ceratocampinae (Lepidoptera: Saturniidae) é a segunda subfamília mais diversa de Saturniidae com 300 espécies descritas em 30 gêneros do sul do Canadá ao norte da Argentina. Espécies desta subfamília estão amplamente distribuídas no Sudeste do Brasil, com muitas endêmicas do Cerrado e importantes como indicadores da qualidade do ecossistema. Espécimes de Ceratocampinae foram coletados no Parque Estadual do Mirador, estado do Maranhão, Brasil. *Adeloneivaia acuta* (Schaus, 1896), *Adeloneivaia schubarti* Barros & O. Mielke, 1970, *Eacles penelope* (Cramer, 1775) e *Megaceresa pulchra* (Bouvier, 1923) são registradas pela primeira vez no estado do Maranhão e Nordeste do Brasil e *Eacles fairchildi* May & Oiticica, 1941 apenas para o Maranhão. O registro de cinco espécies de Ceratocampinae (Saturniidae) aumenta o conhecimento sobre a diversidade e a importância da preservação das espécies dessa subfamília no bioma Cerrado maranhense e na região Nordeste do Brasil.

Palavras-chave: *Conservação; Diversidade; Mariposas; Nordeste do Brasil.*

Introduction

The Cerrado biome, second in area in Brazil with a wide variety of natural resources and unique neotropical plant formations and organisms, is a priority hotspot for conservation (Evangelista et al. 2021, Freitas et al. 2021).

Ceratocampinae are nocturnal moths with long, sphinx-shaped wings in males, adults with fusiform bodies, variable sizes, antennae quadripectinate in the basal half and filamentous in the apical part in males, and generally filamentous in females (Amarillo 2000, Prestes et al. 2009). This subfamily with 300 species described in 30 genera worldwide from southern Canada to northern Argentina and about

85 species in 21 genera in Brazil is the second most diverse of Saturniidae (Albertoni & Duarte 2015, Kitching et al. 2018).

Ceratocampinae species occur frequently in dry and open environments, with insufficient representation in humid tropical forests. This subfamily has ecological importance and may be bioindicators of environmental and climate change (Braga & Diniz 2018). The polyphagy of the Ceratocampinae larva provides the adaptation of species of this subfamily to several species of host plants, both natural and cultivated, being considered pests of forest crops, including *Eacles imperialis magnifica* Walker, 1856, the most known defoliator of this subfamily and pets of coffee plants (Prestes et al. 2009, Kowalczuck et al. 2012).

The objective is to report new records of Ceratocampinae species for the Cerrado biome in Maranhão state of the Northeast region of Brazil.

Material and Methods

Ceratocampinae species were collected in the Parque Estadual do Mirador between the sources of the Itapecuru and Alpercatas rivers (06°10'S, 044°43'W and 06°42'S,045°54'W) in the municipalities of Fernando Falcão, Formosa da Serra Negra and Mirador, Maranhão, Brazil. The vegetation of this park is of the Cerrado type with a sub-humid climate, annual rainfall of 1,200 to 1,400 mm and average maximum and minimum temperatures of 33°C and 19°C, respectively (Silva et al. 2020).

Ceratocampinae individuals were collected between 6:00 P.M. and 6:00 A.M. from October 2006 to March 2012 using a light trap with a white sheet (3 × 2 m) and a 250-watt mercury vapor lamp (UV) during waning or new moon nights. The insects were sacrificed with the injection of 1 ml of ammonia in their thorax. In laboratories, the individuals were mounted on specific boards with the fixation of entomological pins, remaining for 20 days, for dehydration at room temperature, after this period, labelled with information on the location and date of collection. These individuals were identified based on their external morphology, genitalia dissection and in the literature (Lemaire 1988) and deposited and preserved dry in the Zoological Collection of Maranhão, Brazil (CZMA), at the State University of Maranhão, on the Caxias campus.

Results and Discussion

Adeloneivaia acuta (Schaus, 1896), *Adeloneivaia schubarti* Barros & O. Mielke, 1970, *Eacles penelope* (Cramer, 1775) and *Megaceresa pulchra* (Bouvier, 1923) (Figure 1) are new records for the Cerrado biome in the Maranhão state and the Northeast region and *Eacles fairchildi* May & Oiticica, 1941 (Figure 2) only for Maranhão, Brazil.

The new records of *A. acuta*, *A. schubarti*, *E. fairchildi*, *E. penelope*, *M. pulchra*, for the Cerrado biome of Maranhão and Northeast Brazil, indicate the need of additional studies on the diversity of Ceratocampinae in this state, biome and region. Fifty-two species of Ceratocampinae were reported for the Brazilian Cerrado with 15 collected in this biome in the Bahia and Maranhão states in Northeast Brazil (Camargo & Becker 1999), with the description of *Citheronula maranhensis* Brechlin & Meister, 2014, *Citheronia phomaranhensis* Brechlin, 2019, *Ptiloscola maranhensis* Brechlin, 2017 and *Schausiella maranhensis* Brechlin & Meister, 2013 for the state of Maranhão, nineteen species of Ceratocampinae are known in the Cerrado of the Northeast Region, demonstrating the limited knowledge about the moth fauna in this state and region (Brechlin & Meister 2013, 2014, Brechlin 2017, Brechlin et al. 2019). *Adeloneivaia schubarti*, *E. fairchildi*, *M. pulchra* have been recorded in the Cerrado of the Midwest and Southeast Brazil (Camargo & Becker 1999) and *A. acuta* and *E. penelope* in the Cerrado, Amazon and Atlantic Forest biomes (Lemaire 1988, Camargo & Becker 1999, Miranda et al. 2015). The diversity of vegetation in the Cerrado and its proximity to other biomes, such as the Amazon Forest and the Caatinga, facilitate the adaptation of species to that biome, because those of different phytophysiognomies of the Cerrado present biogeographic affinity with other biomes, facilitated by their polyphagy (Camargo 2001, Braga & Diniz 2015). Deforestation reduces diversity and increases the need of conservation programs (Correa-Carmona et al. 2021) in the Cerrado and in other biomes in the Northeast region of Brazil, such as the Caatinga (Câmara et al. 2017). The diversity of Saturniidae, including species of the Ceratocampinae, is poorly known in the Cerrado (Camargo 2004).

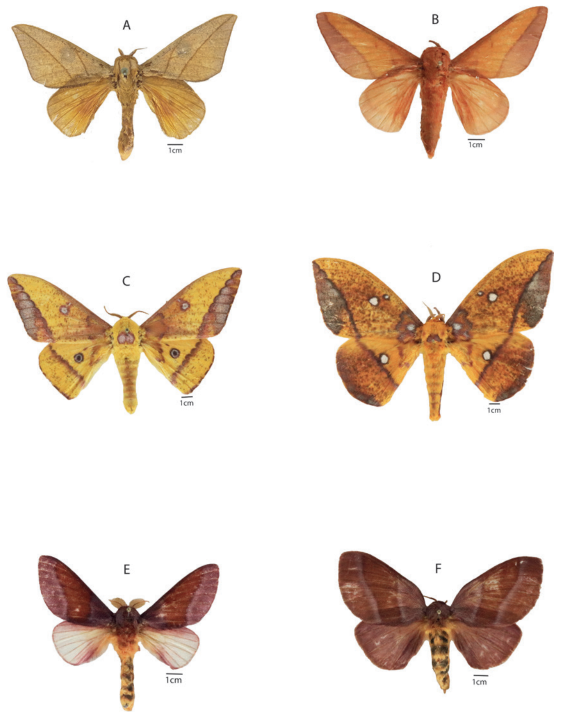
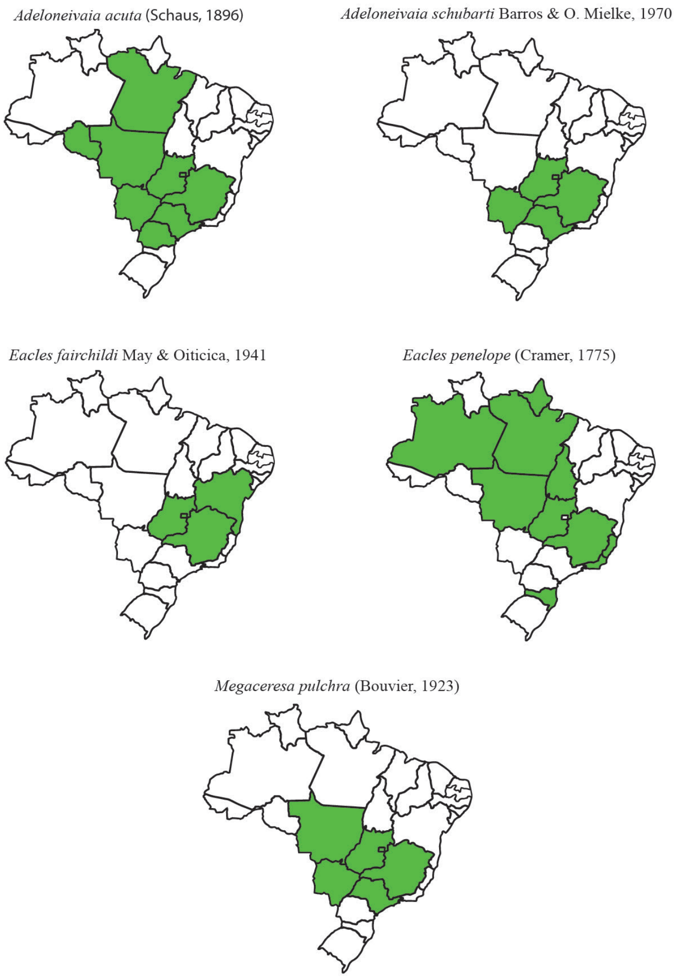


Figure 1. *Adeloneivaia acuta* (male) (A), *Adeloneivaia schubarti* (male) (B), *Eacles fairchildi* (male) (C), *Eacles penelope* (male) (D), *Megaceresa pulchra* (male) (E), *Megaceresa pulchra* (male) (F) (Ceratocampinae: Lepidoptera: Saturniidae) as new records for the Cerrado biome of the Maranhão state and the Northeast region of Brazil.

New Records of Ceratocampinae Species for the for State of Maranhão and Northeast Brasil

1. *Adeloneivaia acuta (Schaus, 1896) (Figure 1A) (Figure 2)*

Distribution: Brazil (Federal District, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Rondônia and São Paulo), Colombia, Ecuador, Peru and Venezuela (Lemaire 1988, Marinoni



Adeloneivaia acuta (Schaus, 1896)

Adeloneivaia schubarti Barros & O. Mielke, 1970

Eacles fairchildi May & Oiticica, 1941

Eacles penelope (Cramer, 1775)

Megaceresa pulchra (Bouvier, 1923)

Figure 2. Geographic distribution of *Adeloneivaia acuta*, *Adeloneivaia schubarti*, *Eacles fairchildi*, *Eacles penelope*, *Megaceresa pulchra* in Brazil.

et al. 1997, Camargo & Becker 1999, Racheli & Racheli 2005a, 2005b, Decaëns et al. 2007, Miranda et al. 2015).

New record for the state of Maranhão and Northeast Brasil.

Host plants: *Acacia baileyana* F. Muell (Fabaceae) (Mejia et al. 2020).

2. *Adeloneivaia schubarti Barros & O. Mielke, 1970 (Figure 1B) (Figure 2)*

Distribution: Brazil (Federal District, Goiás, Mato Grosso do Sul, Minas Gerais and São Paulo) (Lemaire 1988, Camargo & Becker 1999, Camargo & Schmidt 2009, Miranda et al. 2015).

New record for the state of Maranhão and Northeast Brazil.

Host plants: *Stryphnodendron adstringens* (Mart.) Coville (Fabaceae) (Diniz et al. 2001, Furtado 2001, Diniz et al. 2013, Mejia et al. 2020).

3. *Eacles fairchildi May & Oiticica, 1941 (Figure 1C) (Figure 2)*

Distribution: Brazil (Bahia, Goiás, Federal District and Minas Gerais) (Lemaire 1988, Camargo & Becker 1999, Camargo & Schmidt 2009, Miranda et al. 2015).

New record for the state of Maranhão, Brazil.

Host plants: no information.

4. *Eacles penelope (Cramer, 1775) (Figure 1D) (Figure 2)*

Distribution: Bolivia, Brazil (Amapá, Amazonas, Espírito Santo, Goiás, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro, Santa Catarina and Tocantins), Colombia, Ecuador, Guyana, French Guiana, Panama, Peru and Suriname (Lemaire 1988, Camargo & Becker 1999, Racheli & Racheli 2006, Hawes et al. 2009, Miranda et al. 2015).

Host plants: *Lithraea brasiliensis* Marchand, *Malosma laurina* (Nutt) Abrams, *Schinus polygamus* (Cav.) Cabrera e *Schinus terebinthifolius* Raddi (Anacardiaceae), *Liquidambar styraciflua* L. (Altingiaceae), *Fagus sylvatica* L., *Quercus ilex* L. (Fagaceae), *Tripodanthus acutifolius* (Ruiz & Pav.) (Loranthacea), *Psidium guajava* L. (Myrtaceae), *Zea mays* L. (Poaceae) e *Salix caprea* L. (Salicaceae) (Mejia et al. 2020).

5. *Megaceresa pulchra (Bouvier, 1923) (Figure 1E, F) (Figure 2)*

Distribution: Brazil (Federal District, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais and São Paulo) and Paraguay (Lemaire 1988, Camargo & Schmidt 2009, Díaz & Smith 2013, Miranda et al. 2015).

New record for the state of Maranhão and Northeast Brazil.

Host plants: *Anadenanthera peregrina* (L.) Speg e *Calliandra parviflora* Benth (Fabaceae) (Mejia et al. 2020).

Conclusion

The register of five species of Ceratocampinae as new occurrences expands knowledge to 13 species known from the Cerrado of Maranhão and 23 species from the Cerrado biome of Northeast Brazil.

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Author Contributions

Alberico Alves dos Santos: manuscript preparation.

Carlos Alberto Domingues da Silva: contributed to revision of the manuscript.

Roberto da Silva Camargo: contributed to revision of the manuscript.

Carlos Frederico Wilcken: contributed to revision of the manuscript.

Rodrigo Almeida Pinheiro: contributed to revision of the manuscript.

Pedro Guilherme Lemes: contributed to revision of the manuscript.

José Cola Zanuncio: contributed to writing and revision of the manuscript.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This research did not involve actions with human beings and/or clinical trials to be approved by an Institutional Committee.

Data Availability

Supporting data are available at <https://doi.org/10.48331/scielodata.YRGRJ0>.

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Short Communication

Rediscovery of presumably extinct species of *Aristida* in São Paulo State, Brazil

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Abstract: Two species of Poaceae (Aristidoideae) *Aristida ekmaniana* Henrard and *A. macrophylla* Hack. considered "presumably extinct" in the Brazilian state of São Paulo were rediscovered during fieldwork. We hereby describe the location, ecosystem, and *habitat* type where the species were found. We suggest these grasses be removed from the list of extinct species and be placed in a category compatible with the current knowledge about their conservation status in the state of São Paulo.

Keywords: *Aristidoideae; native grass; Poaceae.*

Redescoberta de espécies presumivelmente extintas de *Aristida* no estado de São Paulo, Brasil

Resumo: Duas espécies de Poaceae (Aristidoideae), *Aristida ekmaniana* Henrard e *A. macrophylla* Hack., consideradas "presumivelmente extintas" no estado de São Paulo, Brasil, foram redescobertas durante trabalho em campo. Descrição, ilustração e observações ecológicas são apresentadas, incluindo locais de observação, ecossistemas e habitats. Sugerimos a revisão do status de conservação das espécies no estado de São Paulo.

Palavras-chave: *Aristidoideae; gramínea nativa; Poaceae.*

Introduction

Aristida L. (subfamily Aristidoideae) is a worldwide grass genus of annual and/or perennial plants containing almost 305 species distributed in grasslands, deciduous forests, arid and semi-arid ecosystems of the tropical and subtropical areas around the globe (Gallaher et al. 2022, Cerros-Tlatilpa et al. 2011). It is a monophyletic genus that include C3 and C4 grass species (Gallaher et al. 2022). In Brazil, *Aristida* native species can be easily recognized in the field by the lemma with 3 awns and uniflorous spikelets. Most species of *Aristida* have a peculiar Kranz anatomy, with double concentric layers of chlorenchyma cells formed by a bundle sheath containing most of the chloroplasts, surrounded by an outer layer consisting of a small number of mesophyll cells (Longhi-Wagner 1999, Cerros-Tlatilpa et al. 2011, Gallaher et al. 2022). The non-Kranz species is *A. longifolia* Trin. (Cerros-Tlatilpa & Columbus 2009).

Aristida species are important components of pastures, savannas, dry forests, deserts, and abandoned areas (de Winter 1963, Simon 1992, Freeman 2009, Fatima et al. 2018). Although *Aristida* displays considerable importance in the structural diversity of many biomes they can be harmful to the livestock and wildlife (Stubbendieck et al. 1992, Lazarides 2002).

The genus has four diversity centers – Africa, North America, South America, and Australia (de Winter 1965). They are especially abundant in Brazil, comprising 40 species, 11 of which are endemic (Longhi-Wagner 2020). *Aristida* species grow in anthropic areas, Caatinga (*sensu stricto*), grasslands vegetation on top of hills, floodplains, and

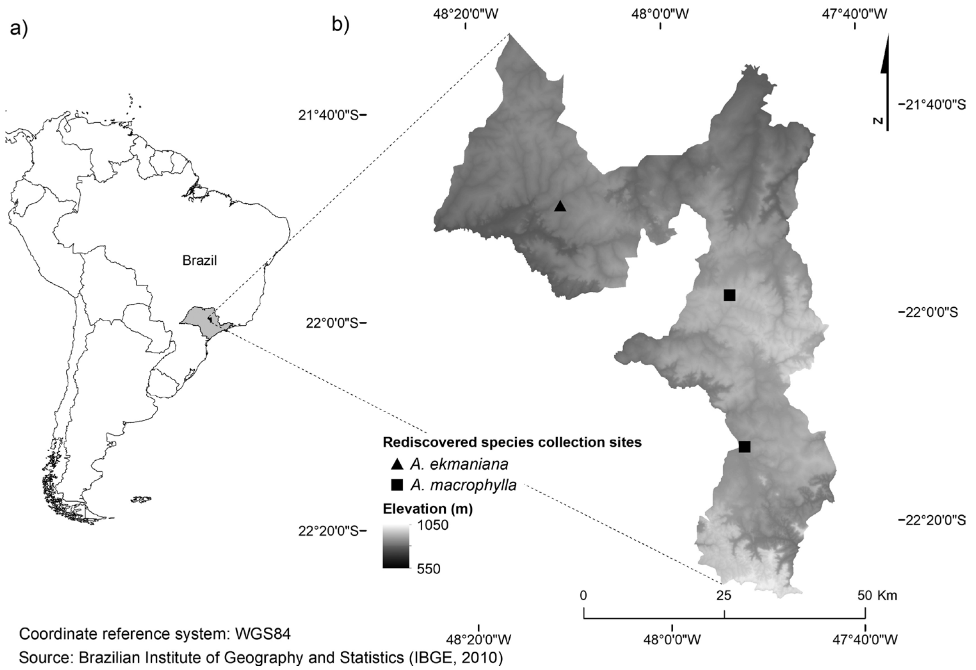

Figure 1. (a) Geographic area where the populations of *Aristida ekmaniana* Henrard and *A. macrophylla* Hack were registered in the state of São Paulo; (b) locations where specimens of *A. ekmaniana* and *A. macrophylla* were collected.

rocky fields, Cerrado (*sensu lato*) (Savanna), and Amazonian Savanna (Flora e Funga do Brasil 2023). In the state of São Paulo there are 18 native species (Longhi-Wagner 2020), of which eight are considered threatened in the state list (São Paulo-SMA 2016).

Cerrado is the most critically threatened domain in Brazil (Lopes et al. 2021). The main causes are loss of native vegetation due to land conversion to pasture and agriculture and invasion by African grasses (Pivello et al. 1999, Durigan et al. 2007, Strassburg et al. 2017, Lopes et al. 2021). Habitat loss is one of the largest current threats to the planet, causing biodiversity loss and species extinction (Roberts et al. 2021).

During field works in Cerrado areas in São Paulo in 2022, some individuals of Poaceae were collected, including two *Aristida* species listed as "presumably extinct" (EX) in the official list of endangered species in the State (São Paulo-SMA 2016). This study approaches the rediscovery of these species in the state of São Paulo.

Material and Methods

Field expeditions were carried out in 2022 in the central region of the state of São Paulo (Figure 1), where specimens of *Aristida* were collected and identified in uncovered soil, anthropic grasslands, and roadside areas. Fertile specimens were collected later, in December of 2022, to confirm the identification. The collected material was identified using the identification and description key from Wanderley et al. (2001) and Flora e Funga do Brasil (2023). The morphologic terminology follows Longhi-Wagner (1990, 1999).

The material was collected following the usual phanerogamic taxonomy procedures (Fidalgo & Bononi 1989) and using a Garmin® GPS device; complementary coordinates were obtained through Google Earth®. The material was deposited at the Maria Eneyda P. Kaufmann Fidalgo Herbarium – SP, at the Environmental Research Institute of São Paulo.

The climate and soil type characteristics at the locations where the specimens were found were obtained from specific maps. The climate types followed Köppen classification (Alvarez et al. 2013) and the soil types followed Brazilian Soil Classification System (Oliveira et al. 2000; Santos et al. 2018).

Assessment of the conservation status was made using the IUCN Standards and Petitions Comitee (2022) categories and criteria; the extent of occurrence (EOO) and area of occupancy (AOO) were determined with GeoCat (Bachman et al. 2011). The evaluation included new and old collections of both species whose data were available at Species Link data base and Herbarium SP.

Results and Discussion

We registered the occurrence of *Aristida ekmaniana* and *A. macrophylla* – considered "presumably extinct" according to Resolução SMA # 57 from June 5, 2016, from the Secretariat of the Environment (São Paulo-SMA 2016) in distrophic soils (dystrophic *Neossolos Quartzarênicos* and dystrophic *Latossolos*) (Oliveira et al. 2000) at altitudes from 569 to 861 m.a.s.l. within the Cerrado domain, in Cwa dry-winter humid subtropical climate, according to Köppen's climate classification (Alvares et al. 2013). (Table 1).

Aristida ekmaniana Henrard (1926: 54). (Figure 2).

Perennial, caespitose, (58-) 60-85 (-115 cm) tall. Sheaths glabrous to sparsely pilose; ligule ca. 0.2 mm, membranous-ciliated, short membranous at the base and long ciliated at the apex; blade (7-)11-34 cm long, 0.1-0.36 cm wide, linear-lanceolate, with leaf dimorphism, basal ones flat and curved when old, upper blades conduplicate and erect. Panicle contracted, 15-33 cm long, subdense, part interrupted, leaving the rachis visible. Glumes acute, the lower ones (6-)9.8-14.2 mm long, generally longer, rarely subequal or shorter than the upper

Table 1. List of rediscovered species and registration number (collector and voucher), location of collection, altitude, and substrate in which they were found.

Taxa	Collector(s), number and collection date	Voucher	Specimen collection sites (rediscovery)	Altitude (m.a.s.l.)	Köppen climate type*	Habitat	Substrate**
Aristida ekmaniana Henrard	*L.D. Sanglade & L.L. Vituri 9,* 23-III-2022	SP 526126	BRAZIL. SÃO PAULO: Araraquara, SP-310, km 271, 21°49'17,4"S, 48°10'46,9"W	661	Cwa	roadside area	clayish, dystrophic Latossolo
Aristida macrophylla Hack	*L.D. Sanglade & L.L. Vituri 6,* 09-VIII-2022	SP 526128	BRAZIL. SÃO PAULO: São Carlos, Pedro Muskat Street, no number, 21°58'7,3"S, 47°53'22,4"W	861	Cwa	roadside area	clayish, dystrophic Latossolo
	L.D. Sanglade & L.L. Vituri 7, 09-VIII-2022		BRAZIL. SÃO PAULO: Itirapina, SPA-097/225, km 5, 22°12'40,4"S, 47°52'6,1"W	739	Cwa	anthropic grassland	sandy, dystrophic Neossolo Quartzarênico

*Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L.M.; Sparovek, G. 2013. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift, v. 22, n. 6, p. 711-728. **Oliveira, J., Camargo, M., Calderano Filho, B. and Rossi, M. 2000. Mapa Pedológico do Estado de São Paulo. O Agronômico 52, 21–23.

Figure 2. *Aristida ekmaniana* Henrard. – A. Habit. – B. detail of glabrous sheath and tuft of trichomes on adaxial base. – C. detail of sheath with glabrous neck and base of the leaf blade with sparse trichomes. – + e * = fragment of the synflorescence. – D. spikelets. – E. upper glume. – F. lower glume. – G. lemma with column. – H. callus. (*Sanglade & Vituri 10* SP).

ones (5-)8.5-14 mm long and may vary within the same panicle. Lemma 6-7(-9) mm long (including (0.8-)1-1.2 mm acute callus); column 8-12 mm long, without a node of articulation at the apex, without ventral longitudinal groove, awns subequal, straight or slightly twisted at base, the central one 15-22 (-30) mm long, the lateral ones 13-25 mm long. Caryopsis with superficial ventral longitudinal groove.

The specimen recently collected from Araraquara presented subequal glumes (5-6 mm) and short column with 4-5 mm long. The set of characteristics of the lemma column length, callus morphology and inflorescence distinguish this species from the most similar ones.

Examined material: *BRAZIL. SÃO PAULO: Araraquara,* 23-III-2022, *L.D. Sanglade & L.L. Vituri 9,* SP-310, km 271, 21°49'17.4"S, 48°10'46.9"W, 661 m.a.s.l., Cwa, clayish dystrophic Latossolo in roadside area*;* Itirapina, 25-III-1963, T. Sendulsky 90, 5 km along road Washington Luiz – Rio Claro (road side); São José dos Campos, 31-V-1961, G. Eiten & T. Sendusky 2850, disjunct cerrado of several hundred sq.km surrounded by former forest. Ca. 7 km S of main plaza of São José dos Campos, along road to Paraibuna. Cerrado with trees to 5 m tall, 5-15 m apart, plus scattered shrubs & grasses. Soil light brown fine sand clay; id. 31-V-1961, G. Eiten & T. Sendusky 2859, 5.5 km S & 1.9 km E of main plaza in city of São José dos Campos (along road to Paraibuna). Cerrado low woodland with trees 3-5 m tall 5-15 m apart, scattered shrubs & grasses, soil light brown fine sandy clay.

Distribution, ecology, and conservation: Endemic to Brazil, confirmed for cerrado (*sensu lato*) in the Northeast region (BA, RN), Central-West Region (DF, GO, MT), Southeast (MG, SP), and South (PR) (Longhi-Wagner 2020). In this work, the species was newly registered in the municipality of Araraquara. In the state of São Paulo, the extension of occurrence (EOO) is 7,708 km² and the occupation area is 16 km². Until now, collection from only four locations have been registered – those from São José dos Campos are from 1961 and from Itirapina, from 1963. All locations are within or relatively close to urban areas and intensely affected by the presence of African Poaceae. The population is greatly fragmented and distant (at least 150 km) from places where the species was registered in the neighboring states of Minas Gerais and Paraná.

This species has not been evaluated at national level yet. Considering the new collection, for the state of São Paulo we suggest that

Figure 3. *Aristida macrophylla* Hack. – A. Habit. – B. detail of sheath with glabrous neck and membranous-ciliated ligule. – CD. fragment of the subdensiflora panicle, interrupted. – E. lower glume longer than upper glume. – F. upper glume. – G. lemma with column. – H. callus. (*Sanglade & Vituri 6* SP).

it is downgraded from "presumably extinct" category, to "endangered" [EN B2ab(i,ii,iii,iv)].

Aristida macrophylla Hack. (1906: 16). (Figure 3).

Perennial, caespitose, (-0.3) 0.5-1 m tall. Sheaths with glabrous neck, glabrous margin or with sparse trichomes at the base; hairy ligule, 0.5-0.8 mm long; blade 15-50 (-55) cm long, (0.08-) 0.15-0.25(-3) cm wide, glabrous or with sparse trichomes at the base of the adaxial surface, linear, without leaf dimorphism, conduplicate or convoluted, usually flexuous. Panicle contracted to subarbertate, (-14) 18-23 (-42) cm long. Glumes acute, the lower ones (9-)10-14(-16) mm long, longer than upper ones (6-)10-12 mm long. Lemma 6-7(-10) mm long (including 0.5-0.7 mm subacute callus), with ventral longitudinal groove; column (2-)5-7(8-) mm long, without a node of articulation at the apex; awns subequal or central longer, the central one 16-24(-28) mm long, the lateral ones 14-21(-22) mm long, connivent at the base 1-3 mm, then divergent, straight or flexuous. Caryopsis grooved.

The examined materials differed somewhat in measurements. L.D. Sanglade & L.L. Vituri 6 presented lower glume a little smaller (9 mm) than the average described 10-14(-16) mm and the column was a little smaller (2.5 mm) in relation to the average 5-7(- 8) mm. Sanglade, L.D. & Vituri, L.L. 07 had an inflorescence 42 cm long, blade 0.3 mm wide and the column was also smaller (0.2 mm long), with the central awn longer up to 28 mm and the side ones 22 mm long.

Examined material: *BRAZIL. SÃO PAULO: São Carlos*, 09-VIII-2022, *L.D. Sanglade & L.L. Vituri 6*, Rua Pedro Muskat, 21°58'7.3"S, 47°53'22.4"W, 861 m.a.s.l., Cwa, clayish dystrophic Latossolo in roadside area, SP 526128; *Itirapina*, 09-VIII-2022, *L.D. Sanglade & L.L. Vituri 7*, SPA 097/225, km 5, 22°12'40.4"S, 47°52'.1"W, 739 m.a.s.l., Cwa, sandy dystrophic Neossolo Quartzarênico in anthropic grassland; *Itirapina,* 23-III-1963, *T Sendulsky 713*, along road Washington Luiz, SP66011; *Capão Bonito*, 10-X-1966, *J. Mattos 13979*, Capão Bonito-Itararé highway, in campo sujo vegetation, SP102041; *São Paulo*, 31-X-1947, *A. Brandão Joly* 511, Butantan, grassland, SP69854.

Distribution, ecology, and conservation: This species occurs in Argentina, Paraguay, and Brazil and was confirmed in the Southeast (SP) and South Region (PR, SC, RS). It grows on grasslands in the Cerrado, Atlantic Forest, and Pampa domains (Longhi-Wagner 2020). In the state of São Paulo, it was collected in São Paulo metropolitan region, where its type comes from (Pilar, in Ribeirão Pires) in 1902, and in the municipality of São Paulo in 1947 and in Itapetininga in 1887, Capão Bonito and Itirapina in the 1960's, thus totaling 5 locations, all in currently threatened areas. Recent collections were done in São Carlos (2007 and 2022) and Itirapina. The areas of occurrence either have already or are becoming urban areas and are affected by the presence of African Poaceae.

Its risk of extinction has not been evaluated in Brazil yet. Because its occupation area extends 32 km² in the state of São Paulo and its population is greatly fragmented and threatened, we suggest the removal of the species from the "presumably extinct category", to be reclassified as "endangered" [EN B2ab (i,ii,iii,iv)].

The long time without collections of these Poaceae species classified as presumably extinct in the state of São Paulo, together with other recent rediscoveries (Filgueiras & Shirasuna 2009, Rodrigues & Filgueiras 2013), may be resultant to the fact that they are under-collected due to difficulty of non-expert to distinguish them from ruderal or invasive species. Another reason may be a certain bias that botanists have in not collecting in areas where the native vegetation, especially grasslands, is disturbed, but which still allow the growth of native rare species. This situation also brings to light that sampling deficiency interfere with a precise assessment of conservation status of many species and hinder the identification of priority conservation areas.

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Authors Contributions

Lucas Dias Sanglade: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation; and contribution to critical revision, adding intellectual content.

Maria Tereza Grombone Guaratini: Substantial contribution in the concept and design of the study; contribution to data analysis and interpretation; contribution to manuscript preparation; and contribution to critical revision, adding intellectual content.

Cíntia Kameyama: Substantial contribution in the concept and design of the study; contribution to data analysis and interpretation; contribution to manuscript preparation; and contribution to critical revision, adding intellectual content.

Regina Tomoko Shirasuna: Contribution to data analysis and interpretation; contribution to manuscript preparation; and contribution to critical revision, adding intellectual content.

Raquel Stucchi Boschi: Contribution to data collection; contribution to manuscript preparation; and contribution to critical revision, adding intellectual content.

Dalva Maria da Silva Matos: Contribution to critical revision, adding intellectual content.

Vânia Regina Pivello: Contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by a Institutional Committee.

Data Availability

The exsiccates were deposited at the Maria Eneyda P. Kaufmann Fidalgo Herbarium – SP, at the Botanical Institute of São Paulo. The primary data analyzed during the current study is reported in the main text as Table 1. The authors confirm that all data necessary for reproducing the study findings are available in the designated dataset.

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Inventory

Butterflies (Lepidoptera: Papilionoidea) of Iguaçu National Park and surrounding areas in southern Brazil: a long-term survey, with six new records for the Brazilian fauna

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Abstract: Iguaçu National Park is the second largest (1852.62 km²) protected area in the Atlantic Forest domain and harbors the largest area of semideciduous seasonal forest in Brazil. In this study, we present 795 subspecies and 787 species of butterflies that occur in this protected area and its surrounding areas, collected over 15 years and ten months using different non-standardized sampling methods. We also searched for additional records in the literature, entomological collections, and citizen science platforms on the internet. Among the sampled taxa, six are recorded for the first time in Brazil: *Emesis orichalceus* Stichel, 1916, *Theope p. pakitza* Hall & Harvey, 1998 (Riodinidae), *Elbella v. viriditas* (Skinner, 1920), *Apaustus gracilis* ssp. n. (Hesperiidae), *Deltaya* sp. n. (Nymphalidae), and *Symbiopsis* sp. n. (Lycaenidae). Another six are listed as endangered in lists of butterflies of conservation concern. The records for some species significantly increase previously documented distributions.

Keywords: *Atlantic Forest; biodiversity; conservation; endangered species; Neotropical region.*

As Borboletas (Lepidoptera: Papilionoidea) do Parque Nacional do Iguaçu e arredores no Sul do Brasil: um inventário de longo prazo, com seis novos registros para a fauna brasileira

Resumo: O Parque Nacional do Iguaçu é a segunda maior Unidade de Conservação (1.852,62 km²) no domínio Mata Atlântica, abrigando a maior área de Floresta Estacional Semidecídua no Brasil. Neste estudo apresentamos uma lista com 795 subespécies e 787 espécies de borboletas que ocorrem nesta Unidade de Conservação e seus arredores, coligida ao longo de 15 anos e dez meses através do uso de diferentes métodos de amostragem não padronizados. Nós também procuramos por registros adicionais na literatura, coleções entomológicas e plataformas de ciência cidadã na internet. Dentre os táxons amostrados, seis são registrados pela primeira vez para o Brasil: *Emesis orichalceus* Stichel, 1916, *Theope p. pakitza* Hall & Harvey, 1998 (Riodinidae), *Elbella v. viriditas* (Skinner, 1920), *Apaustus gracilis* ssp. n. (Hesperiidae), *Deltaya* sp. n. (Nymphalidae) e *Symbiopsis* sp. n. (Lycaenidae). Outras seis espécies são consideradas ameaçadas de extinção em listas de borboletas de interesse para a conservação. Os registros de algumas espécies aumentam significativamente as suas distribuições previamente documentadas.

Palavras-chave: *biodiversidade; conservação; espécies ameaçadas; Mata Atlântica; região Neotropical.*

Introduction

Species inventories document biodiversity by contributing to taxonomic, ecological, and biogeographical studies, and by providing foundational data for management plans and other conservation actions (Brown Jr. & Freitas 1999, Lewinsohn et al. 2005, Santos et al. 2008). Inventory data help document distributions of species and decrease the Wallacean shortfall (Lomolino 2004, Whittaker et al. 2005). They provide data for studies in community ecology and biogeography (e.g., Robbins et al. 1996, Brown Jr. & Freitas 2000, Gonçalves-Souza et al. 2014, Zellweger et al. 2017). Scientifically undescribed taxa may be discovered (e.g., Biezanko & Mielke 1973, Núñez-Bustos 2008, Dolibaina et al. 2011, Lamas et al. 2021), thus decreasing the Linnean shortfall (Brown & Lomolino 1998). Additionally, since butterflies are good bioindicators, responding quickly to environmental changes, well-documented inventories provide the base data that allow early detection of such changes through monitoring (Freitas et al. 2003, Freitas et al. 2006, Santos et al. 2016).

The Atlantic Forest is one of the most important hotspots of biodiversity in the world, and one of the most threatened Brazilian domains, with only ~11.7% of its original vegetation cover (Ribeiro et al. 2009). Its geographic extent in latitude (3°S to 31°S), longitude (35°W to 60°W) and elevation (0 to 3000 m) (Ribeiro et al. 2009) makes it a diverse domain, with a wide range of climate regimes and environmental heterogeneity. Among all Brazilian domains, the Atlantic Forest has the most representative butterfly inventories (Santos et al. 2008, Shirai et al. 2019), and its regional richness exceeds 2100 species (Brown Jr. & Freitas 2000). Despite these results, more information to better understand patterns of butterfly geographic distributions is needed (Francini et al. 2011, Iserhard et al. 2017).

Iguaçu National Park (hereafter Iguaçu NP) is a protected area in the Atlantic Forest domain that harbors the largest preserved area of semideciduous seasonal forest in Brazil (Urban 2002). Mielke (1968) was the first to publish a butterfly list for the region, with emphasis on Hesperiidae, and recorded 106 species in the municipality of Foz do Iguaçu. Decades later, a Rapid Ecological Assessment (REA), conducted to develop a management plan in this protected area, recorded 257 species of six families of butterflies (Mielke 1998). After that, Graciotim & Morais (2016) published a list with 69 fruit-feeding nymphalid species for this region. The authors sampled using Van Someren-Rydon traps placed along two trails, which represented the two principal phytophysiognomies in the park (Urban 2002, ICMBio 2018b). With further sampling, Santos et al. (2018) updated this list to 104 fruit-feeding nymphalid species. Considering the estimated richness of 700 butterfly species for Iguaçu NP (IBAMA 1999) and the 653 species recorded in Argentina's Iguazú National Park (Núñez-Bustos 2009), it appeared that Iguaçu NP was still under sampled. The purpose of this paper is to remedy this undersampling by producing an exhaustive list resulting from more than 15 years of sampling at Iguaçu NP and its surrounding areas, supplemented by records from the literature and from entomological collections. Our data are intended to contribute both to the taxonomy and ecology of Brazilian butterflies and to be used for conservation decisions in this emblematic National Park of the Atlantic Forest in Brazil.

Material and Methods

1. *Study area*

Iguaçu NP is a Brazilian protected area located in the state of Paraná, between the geographic coordinates of 25º05' and 25º41'S and 53º40' and 54º38'W (*Datum* WGS84) (Figure 1). The park area is 1852.62 km² with a 420 km perimeter. It encompasses six municipalities in the state of Paraná (Céu Azul, Capanema, Matelândia, Serranópolis do Iguaçu, São Miguel do Iguaçu and Foz do Iguaçu) and borders another four (Capitão Leônidas Marques, Lindoeste, Santa Tereza do Oeste and Santa Terezinha de Itaipu). The Iguaçu River separates Iguaçu NP in Brazil from its sister park in Argentina (Iguazú National Park). Five rivers, with their sources outside of the park, flow across the park to the Iguaçu River: Gonçalves Dias, São João, Represa Grande, Silva Jardim and Benjamin Constant. A sixth river, the Floriano River, is the only one situated almost entirely in the park. Geologically, Iguaçu NP is located on the third Paraná plateau, in the Paraná Basin.

The climate in the region is classified as humid subtropical (Cfa) according to Köppen, with mean temperatures below 18°C during the coldest month and above 22°C during the hottest month (Alvares et al. 2013). Annual precipitation varies from 1600 to 1800 mm, and the rains are concentrated mainly during hot months. The dry season is not well defined, and the frequency of frosts is low (Nitsche et al. 2019). According to Google Earth (http://earth.google.com), the elevation of the park varies from 120 m, at the Iguaçu River, to over 700 m at its northeastern extremity. The park is located in the Atlantic Forest domain and is composed of four phytophysiognomies (ICMBio 2018b): 1) the seasonal semideciduous forest (hereafter SSF), 2) the mixed ombrophilous forest (hereafter MOF), 3) the floodplain (hereafter FP), and 4) the open formations (hereafter OF). The SSF occupies 85% of the park area and has two subformations, the submontane (up to 400 m), and the montane (between 400 and 600 m). The MOF has a single subformation, the montane (above 600 m). The FP occurs in small areas, subject to extreme flooding conditions for long periods, and is generally occupied by herbaceous-shrub vegetation. The OF comprises all open vegetation formations of anthropogenic or natural origin (Urban 2002, ICMBio 2018b) (Figure 2). The surrounding areas of the park exhibit a heterogeneous landscape, characterized by forest fragments, extensive areas dedicated to agriculture and raising livestock, and urban areas (ICMBio 2018b).

2. *Sampling*

The faunal list is primarily the result of 15 years and ten months of sampling (September 2007 to July 2023) of adult butterflies by the first author, mainly using entomological nets, but in some situations, also using Van Someren-Rydon (hereafter VSR) traps and the Ahrenholz technique, which was especially useful for sampling Hesperiidae butterflies (Freitas et al. 2021b). A digital camera was also used to record some species. Some immature stages were found, which were then raised in the laboratory until emergence.

In the collection with entomological net, many trails and environments were sampled, in all four phytophysiognomies and throughout the altitudinal range (Table 1). Following Brown Jr. & Freitas (2000), special emphasis was given to sites with resources that attract butterflies, like flowering plants, plant exudates, sunny areas in

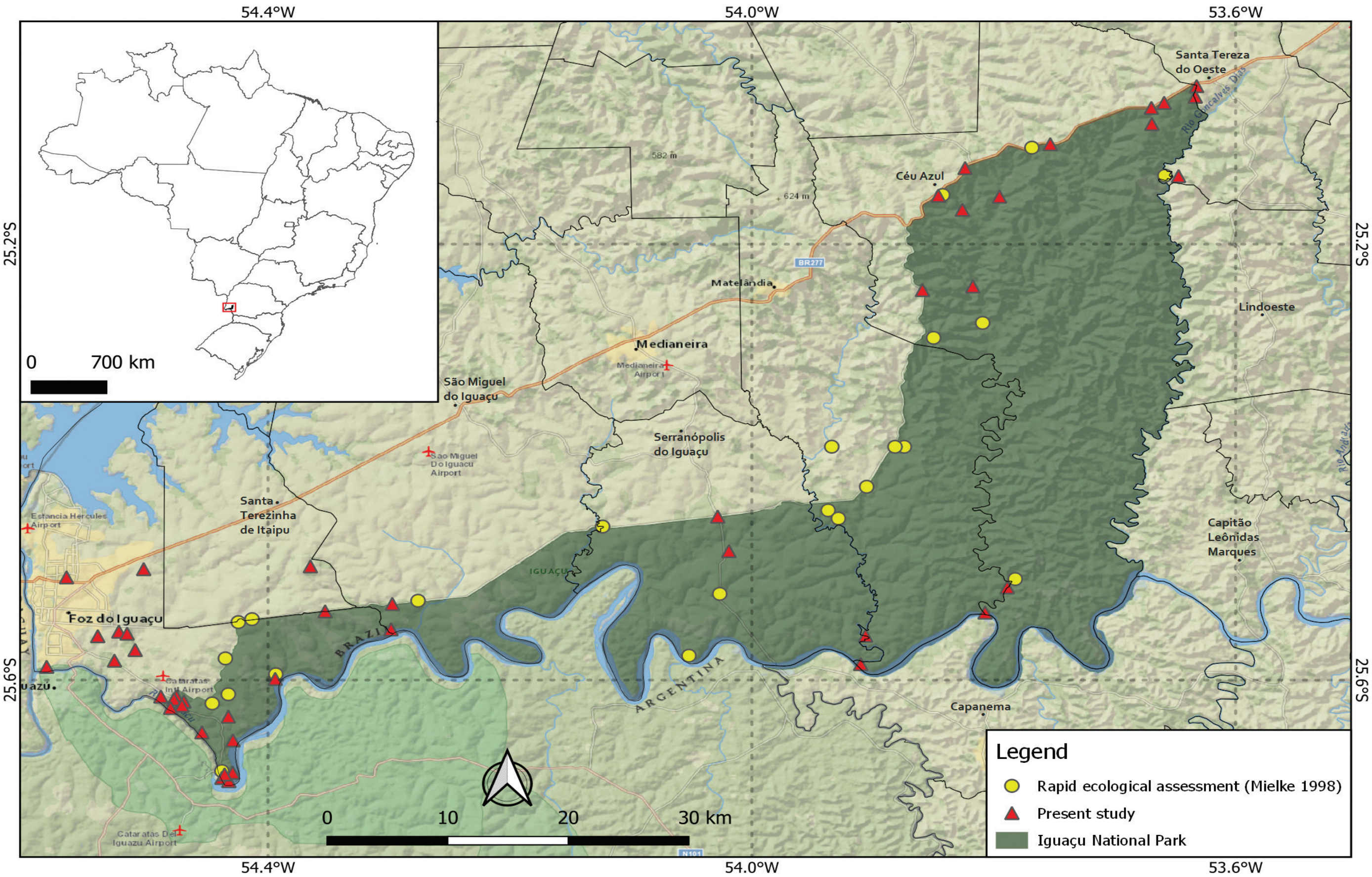

Figure 1. Map of Iguaçu National Park (in dark green) and its location in Brazil, with the main sampling sites; yellow circles = previous surveys by Mielke (1998); red triangles = sites surveyed in the present study.

the interior of the forest, mud puddles, fermented fruits, wet sand along trails or river margins, feces or urine from carnivores, and carcasses. Some sites were more intensively sampled, especially those in the municipality of Foz do Iguaçu. Field sampling was carried out at all seasons, at different times of the day, from 9:00 a.m. to 7:00 p.m., and in all microclimates or habitats within the park and in surrounding areas.

In March 2013, VSR traps baited with a mixture of fermented banana and sugarcane juice were installed on two trails in the Iguaçu NP to sample fruit-feeding butterflies, following a protocol adapted from Uehara-Prado et al. (2005). These trails represent the two principal phytophysiognomies present in the park: 1) an area of SSF, located in the municipality of Foz do Iguaçu, and 2) an area of MOF, located in the municipality of Céu Azul. On each trail, ten traps were placed in line (starting at least 50 m from the forest edge) and with about 20 m between adjacent traps, alternating understory (~1.5 m above the ground) and canopy (~10 m above the ground). The traps remained suspended for two consecutive days on each trail (10 hours of effective sampling per day), resulting in a total sampling effort of 400 trap/hours.

Most Hesperiidae were deposited at the Entomological Collection Padre Jesus Santiago Moure in the Federal University of Paraná (DZUP/UFPR), and specimens of the other families were deposited at the Zoological Collection of the Museu de Diversidade Biológica in the University of Campinas (ZUEC/Unicamp). Some specimens of the genus *Actinote* were deposited at the Entomological Collection of the Museu de Zoologia e Paleontologia in the Federal University of Recôncavo da Bahia (MURB/UFRB).

3. *Species list*

We identified the specimens using taxonomic keys and species guides (e.g., Brown Jr. 1992, Canals 2003, D'Abrera 1984, 1987, 1989, 1994, 1995, Tyler et al. 1994, Klimaitis et al. 2018). We also compared specimens to images of type specimens of American butterflies, available in the *Butterflies of America* database, on internet (Warren et al. 2016), and to species maintained in reference collections (DZUP/UFPR and ZUEC/Unicamp). For some individuals, we examined the genitalia and, more rarely, we used barcoding sequences to determine the species. We also consulted specialists to help us determine specific groups of butterflies (see "Acknowledgements"). For recorded subspecies with sympatric distribution, we use an "x" to indicate that two phenotypes (and sometimes the putative hybrids) are present.

Besides sampling, we compiled data from the literature (Mielke 1968, Jenkins 1990, Casagrande & Mielke 1992, Anken 1994, D'Abrera 1995, Mielke 1998, Hall & Harvey 2002, Callaghan 2010, Lourido 2011, Graciotim & Morais 2016) for any of the ten municipalities in the study area, updating the nomenclature when necessary. We also examined scientific collections, where we found species from the study area that were not previously recorded for the park. These include DZUP at UFPR; two local collections in Foz do Iguaçu, the

Figure 2. Landscapes and environments at Iguaçu National Park: A) semideciduous seasonal forest, 200 m; B) mixed ombrophilous forest, over 700 m, with the presence of several individuals of Brazilian pine *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae); C) stony beach on the banks of the Iguaçu River; D) Blue River; E) a dense patch of tree ferns (Cyatheaceae spp.); F) close view of forest understory with young juçara palm *Euterpe edulis* Mart. (Arecaceae).

Table 1. Sampled sites in the present study and in Mielke (1998), ordered from North to South. Nearby points were treated as a single point. In the case of trails, the altitude presented is the simple arithmetic mean between its highest and lowest point. SSFs = Seasonal Semideciduous Forest, subformation submontana; SSFm = Seasonal Semideciduous Forest, subformation montana; MOF = Mixed Ombrophilous Forest; FP = Floodplain; OF = Open formations.

Name	Phytophysiognomy	Present study	Mielke 1998	Municipality	Coordinates	Altitude
Pousada Eco Vine	MOF, OF	X		Santa Tereza do Oeste	25°03'S; 53°38'W	730 m
Research trail	MOF	X		Céu Azul	25°04'S; 53°39'W	750 m
Fazenda Rio Butu trail	MOF, FP	X		Céu Azul	25°05'S; 53°40'W	710 m
Linha Gonçalves Dias	MOF, OF	X		Santa Tereza do Oeste	25°06'S; 53°38'W	640 m
Abandoned quarry	SSFm	X		Céu Azul	25°06'S; 53°45'W	670 m
North of the municipality of Céu Azul	SSFm		X	Céu Azul	25°06'S; 53°46'W	680 m
Near the Gonçalves Dias River	MOF		X	Céu Azul	25°08'S; 53°39'W	600 m
Boa Vista trail	SSFm	X		Céu Azul	25°09'S; 53°47'W	650 m
Manoel Gomes trail	SSFm, FP	X	X	Céu Azul	25°10'S; 53°49'W	590 m
Jacutinga trail	SSFm	X		Céu Azul	25°14'S; 53°50'W	500 m
Middle course of the Floriano River	SSFm, FP		X	Céu Azul	25°17'S; 53°51'W	540 m
Benjamin Constant River	SSFs		X	Matelândia	25°23'S; 53°53'W	340 m
Bridge over the Silva Jardim River	OF		X	Matelândia	25°23'S; 53°56'W	280 m
Along the Pinheirinho River	SSFs		X	Matelândia	25°25'S; 53°54'W	290 m
Tributary of the Silva Jardim River	SSFs		X	Matelândia	25°26'S; 53°56'W	310 m
Along the Represa Grande River	SSFs		X	Serranópolis do Iguaçu	25°27'S; 54°07'W	220 m
Itaipu Binacional	SSFs, OF	X		Foz do Iguaçu	25°27'S; 54°36'W	120 m
Santa Maria Farm	SSFs, OF	X		Santa Terezinha de Itaipu	25°29'S; 54°22'W	330 m
Near the mouth of the Floriano River	SSFs	X	X	Céu Azul	25°30'S; 53°47'W	280 m
Estrada do Colono	SSFs	X	X	Serranópolis do Iguaçu	25°30'S; 54°01'W	270 m
Aparecidinha neighborhood	OF	X		Foz do Iguaçu	25°30'S; 54°30'W	270 m
Vietnã trail	SSFs, OF	X		Foz do Iguaçu	25°30'S; 54°34'W	200 m
Índio River	SSFs		X	São Miguel do Iguaçu	25°31'S; 54°16'W	210 m
Mouth of the Floriano River	SSFs	X		Capanema	25°32'S; 53°48'W	230 m
Linha Martins	SSFs	X		São Miguel do Iguaçu	25°32'S; 54°18'W	230 m
Estrada Velha de Guarapuava	SSFs, OF	X		São Miguel do Iguaçu	25°32'S; 54°21'W	270 m
Benjamin Constant River Waterfall	SSFs	X		Serranópolis do Iguaçu	25°33'S; 53°54'W	240 m
Cognópolis neighborhood	SSFs, OF	X		Foz do Iguaçu	25°33'S; 54°31'W	210 m
CITI Tênis	SSFs, OF	X		Foz do Iguaçu	25°33'S; 54°32'W	220 m
Iguaçu River lagoon	FP		X	Serranópolis do Iguaçu	25°34'S; 54°03'W	230 m
São João River basin	SSFs		X	Foz do Iguaçu	25°34'S; 54°25'W	220 m
Flora Éden	OF	X		Foz do Iguaçu	25°34'S; 54°30'W	200 m
Poço Preto	SSFs, FP	X	X	Foz do Iguaçu	25°35'S; 54°23'W	190 m
Cataratas Highway near Aquamania	OF	X		Foz do Iguaçu	25°35'S; 54°31'W	190 m
Marco das Três Fronteiras	SSFs, OF	X		Foz do Iguaçu	25°35'S; 54°35'W	140 m
Poço Preto trail	SSFs	X	X	Foz do Iguaçu	25°36'S; 54°26'W	240 m
Escola Parque trail	SSFs	X		Foz do Iguaçu	25°37'S; 54°28'W	210 m
Campinho trail	SSFs, OF	X		Foz do Iguaçu	25°37'S; 54°28'W	190 m
Represa trail	SSFs, FP	X		Foz do Iguaçu	25°37'S; 54°28'W	180 m
Canafístula trail	SSFs	X		Foz do Iguaçu	25°37'S; 54°28'W	190 m
Canzi Hotel trail	SSFs	X		Foz do Iguaçu	25°37'S; 54°29'W	170 m
Old power plant	SSFs	X		Foz do Iguaçu	25°37'S; 54°29'W	150 m
Monitoring trail	SSFs	X		Foz do Iguaçu	25°38'S; 54°26'W	250 m
Bananeiras trail	SSFs, OF	X		Foz do Iguaçu	25°39'S; 54°26'W	210 m
Macuco trail	SSFs	X		Foz do Iguaçu	25°39'S; 54°27'W	180 m
Higrômetro trail	SSFs	X		Foz do Iguaçu	25°41'S; 54°25'W	190 m
Cataratas trail	SSFs	X	X	Foz do Iguaçu	25°41'S; 54°26'W	180 m
Behind the Belmont Hotel	SSFs	X		Foz do Iguaçu	25°41'S; 54°26'W	220 m

Ecomuseum of Itaipu and the Museum of Zoology in the Uniamérica University Center; and two private collections, D.R. Dolibaina and A.D. Warren. We did not include species that could not be identified, as well as literature records for which we did not find voucher material or which may represent species misidentification. In addition, we searched for pictures of butterflies from any of the ten municipalities within and bordering Iguaçu NP on the citizen science platform iNaturalist (https://www.inaturalist.org), Google Images (https://www.google.com/imghp?hl=EN) and Flickr (https://www.flickr.com), but no additional records were obtained.

Pareuptychia summandosa (Gosse, 1880) was considered a junior synonym of *P. ocirrhoe* (Fabricius, 1776) (M.A. Marín, pers. comm.). In the case of *Junonia*, a species complex that has not yet been unveiled, the different sampled phenotypes were grouped under the single taxon *Junonia e. evarete* (Cramer, 1779). Following Freitas et al. (2014), we consider as fruit-feeding species only the nymphalids belonging to the subfamilies Biblidinae (except Eubagini and *Mestra*), Charaxinae, Satyrinae (except non-feeding *Brassolis* and *Dynastor*), and Nymphalinae (including only *Colobura*, *Historis* and *Smyrna*).

We recognized seven butterfly families, including Hedylidae, following recent phylogenetic studies (Kawahara & Breinholt 2014, Breinholt et al. 2018, Espeland et al. 2018). For higher taxonomy within families, we followed Lamas (2004), updated for Nymphalidae (Wahlberg et al. 2009), Riodinidae (Seraphim et al. 2018, Seraphim 2019), and Hesperiidae (Li et al. 2019, Zhang et al. 2019, Cong et al. 2019, Zhang et al. 2022). For generic names, we followed Mielke et al. (2022) and Brockmann et al. (2022) for the subfamily Pyrrhopyginae, Robbins et al. (2022) for the tribe Eumaeini and Espeland et al. (2023) for the subtribe Euptychiina. Taxonomy was also updated for the genera *Morpho* (Blandin 2007, Pablos et al. 2021), *Eryphanis* (Penz 2008), *Zaretis* (Dias et al. 2018), *Phoebis* (Murillo-Ramos et al. 2018), *Agraulis* and *Dryas* (Núñez et al. 2022).

Results

We recorded 787 species (totalling 795 taxa including subspecies) from seven families of Papilionoidea at Iguaçu NP and its surrounding areas (Table 2), consisting of 339 (43.1%) Hesperiidae, 214 (27.2%) Nymphalidae, 115 (14.6%) Lycaenidae, 77 (9.8%) Riodinidae, 24 (3.0%) Pieridae, 17 (2.2%) Papilionidae, and 1 (0.1%) Hedylidae (Figure 3). Of these 795 taxa, 729 were sampled by the first author (including seven only by taking pictures of live specimens), 27 were obtained from the literature and 39 from scientific collections (see “Data Availability” for more details). From the guild of fruit-feeding nymphalids, we recorded a total of 112 species, representing 52.3% of Nymphalidae richness.

The eight species that had more than one recorded subspecies were: 1) *Heliconius ethilla* (Godart, 1819), 2) *Hypothyris euclea* (Godart, 1819), 3) *Tithorea harmonia* (Cramer, 1777) (Nymphalidae), 4) *Ascia monuste* (Linnaeus, 1764) (Pieridae), 5) *Melanis aegates* (Hewitson, 1874), 6) *Rhetus periander* (Cramer, 1777) (Riodinidae), 7) *Saturnus reticulata* (Plötz, 1883), and 8) *Tisias lesueur* (Latreille, [1824]) (Hesperiidae).

We also recorded several taxa that are typical from other domains, such as Amazon and Cerrado. Among typical Amazonian taxa (Díaz

Table 2. List of the butterflies and moth-butterflies (Lepidoptera: Papilionoidea) of Iguaçu National Park and surrounding areas. Species richness for each major taxa are provided within parentheses. * Taxa recorded by the first author solely through photographs of live specimens; ** records from collections or literature (see “Data Availability” for more details); # new records for Brazil; the “x” indicates that phenotypes of two subspecies are present; superscript letters a = the first subspecies correspond to the predominant phenotype; b = very few specimens were collected to determine predominant phenotype; c = there is evidence suggesting that the two subspecies could in fact be two valid species; F = strictly fruit-feeding species (sensu Freitas et al. 2014).

- **PAPILIONOIDEA (787)**
  - **PAPILIONIDAE (17)**
    - **Papilioninae (17)**
      - **Leptocircini (6)**
        - *Mimoides lysithous rurik* (Eschscholtz, 1821)
        - *Mimoides protodamas* (Godart, 1819)
        - *Neographium asius* (Fabricius, 1781)
        - *Protesilaus helios* (Rothschild & Jordan, 1906)
        - *Protesilaus protesilaus nigricornis* (Staudinger, 1884)**
        - *Protesilaus stenodesmus* (Rothschild & Jordan, 1906)
      - **Papilionini (5)**
        - *Heraclides anchisiades capys* (Hübner, [1809])
        - *Heraclides androgeus laodocus* (Fabricius, 1793)
        - *Heraclides astyalus astyalus* (Godart, 1819)
        - *Heraclides hectorides* (Esper, 1794)
        - *Heraclides thoas brasiliensis* (Rothschild & Jordan, 1906)
      - **Troidini (6)**
        - *Battus polydamas polydamas* (Linnaeus, 1758)
        - *Battus polystictus polystictus* (Butler, 1874)
        - *Parides agavus* (Drury, 1782)
        - *Parides anchises nephalion* (Godart, 1819)
        - *Parides bunichus perrhebus* (Boisduval, 1836)**
        - *Parides neophilus eurybates* (Gray, [1853])
  - **LYCAENIDAE (115)**
    - **Polyommatinae (3)**
      - *Hemiargus hanno* (Stoll, [1790])
      - *Leptotes cassius* (Cramer, [1775])
      - *Zizula cyna* (Edwards, 1881)
    - **Theclinae (112)**
      - **Eumaeini (112)**
        - *Allosmaitia strophius* (Godart, [1824])
        - *Arawacus dolylas* (Cramer, [1777])
        - *Arawacus ellida* (Hewitson, 1867)
        - *Arawacus meliboeus* (Fabricius, 1793)
        - *Arawacus separata* (Lathy, 1926)
        - *Arcas imperialis* (Cramer, 1775)
        - *Arzecla arza* (Hewitson, 1874)
        - *Arzecla ceromia* (Hewitson, 1877)
        - *Arzecla nubilum* (Druce, 1907)**
        - *Arzecla tucumanensis* (Johnson & Kroenlein, 1993)
        - *Atlides misma* D’Abrera, 1995
        - *Atlides polybe* (Linnaeus, 1763)
        - *Aubergina vanessoides* (Prittwitz, 1865)
        - *Badecla badaca* (Hewitson, 1868)
        - *Brangas getus* (Fabricius, 1787)
        - *Brangas moserorum* Bálint & Faynel, 2008

Continue...

Table 2. Continuation

Brangas neora (Hewitson, 1867)
Brevianta celelata (Hewitson, 1874)**
Caerofethra carnica (Hewitson, 1873)
Caerofethra eumorpha (Hayward, 1949)
Calycopis bellera (Hewitson, 1877)
Calycopis caulonia (Hewitson, 1877)
Calycopis gentilla (Schaus, 1902)
Calycopis sp.**
Camissecla vesper (Druce, 1909)
Celmia celmus (Cramer, [1775])
Chalybs chloris (Hewitson, 1877)
Chalybs hassan (Stoll, [1790])
Chlorostrymon simaethis (Drury, [1773])
Chlorostrymon telea (Hewitson, 1868)
Contrafacia catharina (Draudt, 1920)
Cupathecla cupentus (Stoll, [1781])
Cyanophrys acaste (Prittwitz, 1865)
Cyanophrys herodotus (Fabricius, 1793)
Cyanophrys pseudolongula (Clench, 1944)**
Cyanophrys remus (Hewitson, 1868)
Decussata empusa (Hewitson, 1867)
Denivia chaluma (Schaus, 1902)
Denivia deniva (Hewitson, 1874)**
Denivia hemon (Cramer, [1775])
Denivia lisus (Stoll, [1790])
Dicya dicaea (Hewitson, 1874)
Electrostrymon endymion (Fabricius, 1775)
Enos thara (Hewitson, 1867)
Erora biblia (Hewitson, 1868)
Erora sp.
Evenus latreillii (Hewitson, 1865)
Evenus regalis (Cramer, [1775])
Gargina gnosia (Hewitson, 1868)
Heterosmaitia marius (Lucas, 1857)
Heterosmaitia palegon (Cramer, [1780])
Heterosmaitia stagira (Hewitson, 1867)
Ignata brasiliensis (Talbot, 1928)
Ignata norax (Godman & Salvin, [1887])*
Ipidecla crepundia (Druce, 1909)
Ipidecla schausi (Godman & Salvin, [1887])
Janthecla aurora (Druce, 1907)
Janthecla rocena (Hewitson, 1867)
Kisutam syllis (Godman & Salvin, 1887)
Kolana chlamys (Druce, 1907)
Kolana ergina (Hewitson, 1867)
Kolana ligurina (Hewitson, 1874)
Laothus phydela (Hewitson, 1867)**
Lathecla mimula (Draudt, 1920)
Magnastigma hirsuta (Prittwitz, 1865)
Marachina asa (Hewitson, 1868)
Mercedes calus (Godart, [1824])
Michaelus ira (Hewitson, 1867)
Michaelus jebus (Godart, [1824])
Michaelus thordesa (Hewitson, 1867)

Continue...

Table 2. Continuation

Ministrymon azia (Hewitson, 1873)
Ministrymon cruenta (Gosse, 1880)
Nesiostrymon calchinia (Hewitson, 1868)
Nesiostrymon tristis (Lathy, 1926)
Nicolaea torris (Druce, 1907)
Ocaria ocrisia (Hewitson, 1868)
Ocaria thales (Fabricius, 1793)
Ostrinotes sophocles (Fabricius, 1793)
Paiwarria aphaca (Hewitson, 1867)
Paiwarria venulius (Cramer, [1779])
Panthiades hebraeus (Hewitson, 1867)
Panthiades phaleros (Linnaeus, 1767)
Paraspiculatus orobia (Hewitson, 1867)
Parrhasius orgia (Hewitson, 1867)
Parrhasius polibetes (Stoll, [1781])
Pseudolycaena marsyas (Linnaeus, 1758)
Rekoa malina (Hewitson, 1867)
Rekoa meton (Cramer, [1779])
Semonina ares (Godman & Salvin, [1887])
Siderus eliatha (Hewitson, 1867)
Strephonota ambrax (Westwood, 1852)
Strephonota elika (Hewitson, 1867)*
Strephonota jactator (Druce, 1907)**
Strephonota tephraeus (Geyer, 1837)
Strymon astiocha (Prittwitz, 1865)
Strymon bazochii (Godart, [1824])
Strymon bubastus (Stoll, 1780)
Strymon cestri (Reakirt, 1867)
Strymon eurytulus (Hübner, [1819])
Strymon megarus (Godart, [1824])
Strymon mulucha (Hewitson, 1867)
Strymon rufofusca (Hewitson, 1877)
Strymon ziba (Hewitson, 1868)
Symbiopsis sp. n.#
Symbiopsis lenitas (Druce, 1907)
Symbiopsis strenua (Hewitson, 1877)
Theclopsis gargara (Hewitson, 1868)
Thepytus thyrea (Hewitson, 1867)
Theritas triquetra (Hewitson, 1865)*
Tmolus cydrara (Hewitson, 1868)
Tmolus echion (Linnaeus, 1767)
Ziegleria hesperitis (Butler & Druce, 1872)

RIODINIDAE (77)

Nemeobiinae (6)

Euselasiini (6)

Euselasia eucerus (Hewitson, 1872)
Euselasia eusepus (Hewitson, 1853)
Euselasia hygenius occulta Stichel, 1919
Euselasia marica Stichel, 1919
Euselasia satyroides Lathy, 1926
Euselasia zara (Westwood, 1851)

Riodininae (71)

Eurybiini (11)

Alesa prema (Godart, [1824])

Continue...

Table 2. Continuation

Eurybia halimede passercula Stichel, 1915
Eurybia pergaea (Geyer, 1832)
Hyphilaria thasus (Stoll, 1780)
Ionotus alector (Geyer, 1837)
Leucochimona icare matatha (Hewitson, 1873)
Mesosemia friburguensis Schaus, 1902**
Mesosemia odice (Godart, [1824])
Mesosemia rhodia (Godart, [1824])
Napaea eucharila (Bates, 1867)
Perophthalma tullius (Fabricius, 1787)
Helicopini (1)
Anteros formosus (Cramer, [1777])
Emesidini (9)
Emesis cerea cerea (Linnaeus, 1767)
Emesis diogenia Prittwitz, 1865
Emesis fastidiosa Ménétriés, 1855
Emesis mandana (Cramer, 1780)
Emesis melancholica Stichel, 1916
Emesis neemias neemias Hewitson, 1872
Emesis ocypore ocypore (Geyer, 1837)
Emesis orichalceus Stichel, 1916#
Emesis russula Stichel, 1910
Nymphidiini (22)
Adelotypa bolena (Butler, 1867)
Ariconias glaphyra (Westwood, 1851)
Aricoris indistincta (Lathy, 1932)**
Aricoris monotona (Stichel, 1910)**
Aricoris signata (Stichel, 1910)
Catocyclotis malca (Schaus, 1902)
Catocyclotis sejuncta (Stichel, 1910)
Joiceya praeclarus Talbot, 1928
Juditha azan azan (Westwood, [1851])
Juditha molpe (Hübner, [1808])
Juditha odites praeclarum (Bates, 1866)
Nymphidium lisimon (Stoll, 1790)
Pseudolivendula hemileuca hemileuca (Bates, 1868)
Synargis calyce (Felder & Felder, 1862)
Synargis ethelinda (Hewitson, 1870)**
Synargis paulistina (Stichel, 1910)
Synargis aff. *regulus* (Fabricius, 1793)
Synargis regulus (Fabricius, 1793)
Teenie argiella (Bates, 1868)
Theope pakitza pakitza Hall & Harvey, 1998#
Theope terambus (Godart, [1824])
Theope thestias Hewitson, 1860
Riodinini (23)
Ancyluris rubrofilum Stichel, 1909
Barbicornis basilis mona Westwood, 1851
Calephelis aymaran McAlpine, 1971
Caria marsyas Godman, 1903
Caria plutargus plutargus (Fabricius, 1793)
Chalodeta theodora (Felder & Felder, 1862)
Chamaelimnas briola doryphora Stichel, 1910
Chorinea amazon amazon (Saunders, 1859)
Detritivora brasilia (Harvey & Hall, 2002)
Inkana incoides (Schaus, 1902)
Lasaia agesilas agesilas (Latreille, [1809])
Lasaia arsis Staudinger, 1888
Lasaia oileus Godman, 1903
Melanis aegates albugo (Stichel, 1910) x *Melanis aegates limbata* (Stichel, 1925)[b]
Melanis marathon charon (Butler, 1874)
Melanis xenia xenia (Hewitson, 1853)
Notheme erota angellus Stichel, 1910
Parcella amarynthina (Felder & Felder, [1865])
Pheles atricolor atricolor (Butler, 1871)
Rhetus periander arthuriana (Sharpe, 1890) x *Rhetus periander eleusinus* Stichel, 1910[a]
Riodina lycisca lycisca (Hewitson, [1853])
Riodina lysippoides Berg, 1882
Syrmatia nyx (Hübner, [1817])
Symmachiini (5)
Mesene aff. *cyneus* (Hewitson, 1874)
Mesene aff. *simplex* Bates, 1868
Mesene monostigma monostigma (Erichson, [1849])
Mesene pyrippe sanguilenta Stichel, 1910**
Pirascca sagaris satnius (Dalman, 1823)
NYMPHALIDAE (214)
Apaturinae (5)
Doxocopa agathina vacuna (Godart, [1824])
Doxocopa kallina (Staudinger, 1886)
Doxocopa laurentia laurentia (Godart, [1824])
Doxocopa linda mileta (Boisduval, 1870)
Doxocopa zunilda zunilda (Godart, [1824])
Biblidinae (40)
Ageroniini (7)
Ectima thecla thecla (Fabricius, 1796)[F]
Hamadryas amphinome amphinome (Linnaeus, 1767)[F]
Hamadryas arete (Doubleday, 1847)*[F]
Hamadryas epinome (Felder & Felder, 1867)[F]
Hamadryas februa februa (Hübner, [1823])[F]
Hamadryas feronia feronia (Linnaeus, 1758)[F]
Hamadryas fornax fornax (Hübner, [1823])[F]
Biblidini (2)
Biblis hyperia nectanabis (Frühstorfer, 1909)[F]
Mestra hersilia apicalis (Staudinger, 1886)**
Callicorini (8)
Callicore hydaspes (Drury, 1782)[F]
Callicore sorana sorana (Godart, [1824])[F]
Catagramma pygas thamyras Ménétriés, 1857[F]
Catagramma pyracmon pyracmon (Godart, [1824])[F]
Diaethria candrena candrena (Godart, [1824])[F]
Diaethria clymena janeira (C. Felder, 1862)[F]
Diaethria eluina eluina (Hewitson, [1855])[F]
Haematera pyrame pyrame Hübner, [1819][F]
Catonephelini (9)
Catonephele acontius caeruleus Jenkins, 1985[F]
Catonephele numilia penthia (Hewitson, 1852)[F]

Continue...

Table 2. Continuation

Cybdelis phaesyla (Hübner, [1831])**[F]
Eunica eburnea Frühstorfer, 1907[F]
Eunica eurota dolores (Prittwitz, 1871)**[F]
Eunica malvina malvina Bates, 1864[F]
Eunica margarita (Godart, [1824])[F]
Eunica tatila bellaria Frühstorfer, 1908[F]
Myscelia orsis (Drury, [1782])[F]
Epiphilini (5)
Epiphile hubneri Hewitson, 1861[F]
Epiphile orea orea (Hübner, [1823])[F]
Nica flavilla flavilla (Godart, [1824])[F]
Pyrrhogyra neaerea arge Gosse, 1880[F]
Temenis laothoe meridionalis Ebert, 1965[F]
Eubagini (9)
Dynamine aerata (Butler, 1877)
Dynamine agacles agacles (Dalman, 1823)
Dynamine artemisia artemisia (Fabricius, 1793)
Dynamine athemon athemaena (Hübner, [1824])
Dynamine coenus coenus (Fabricius, 1793)
Dynamine meridionalis Röber, 1915
Dynamine myrrhina (Doubleday, 1849)
Dynamine postverta postverta (Cramer, 1779)
Dynamine tithia tithia (Hübner, 1823)
Charaxinae (13)
Anaeini (8)
Consul fabius drurii (Butler, 1874)[F]
Fountainea glycerium cratais (Hewitson, 1874)[F]
Fountainea ryphea phidile (Geyer, 1837)[F]
Hypna clytemnestra huebneri Butler, 1866[F]
Memphis acidalia victoria (Druce, 1877)[F]
Memphis moruus stheno (Prittwitz, 1865)[F]
Zaretis hurin Dias, 2018[F]
Zaretis strigosus (Gmelin, [1790])[F]
Preponini (5)
Archaeoprepona chalciope (Hübner, [1823])[F]
Archaeoprepona demophon thalpius (Hübner, [1814])[F]
Archaeoprepona demophoon demophoon (Hübner, [1814])[F]
Prepona laertes (Hübner, [1811])[F]
Prepona pylene laertides Staudinger, 1898[F]
Cyrestinae (3)
Cyrestini (3)
Marpesia chiron marius (Cramer, [1779])
Marpesia petreus petreus (Cramer, [1776])
Marpesia zerynthia zerynthia Hübner, [1823]**
Danainae (24)
Danaini (5)
Danaus eresimus plexaure (Godart, 1819)*
Danaus erippus (Cramer, [1775])
Danaus gilippus gilippus (Cramer, [1775])
Lycorea halia discreta Haensch, 1909
Lycorea ilione ilione (Cramer, [1775])
Ithomiini (19)
Aeria olena olena Weymer, 1875
Brevioleria seba emyra (Haensch, 1905)
Callithomia lenea methonella (Weymer, 1875)
Dircenna dero celtina Burmeister, 1878
Episcada carcinia Schaus, 1902
Episcada hymenaea hymenaea (Prittwitz, 1865)
Epityches eupompe (Geyer, [1832])
Hypothyris euclea laphria (Doubleday, 1847) x *Hypothyris euclea nina* (Haensch, 1905)[a]
Ithomia agnosia zikani d'Almeida, 1940
Ithomia lichyi lichyi d'Almeida, 1939**
Mcclungia cymo salonina (Hewitson, 1855)
Mechanitis lysimnia lysimnia (Fabricius, 1793)
Methona themisto themisto (Hübner, 1818)
Placidina euryanassa (Felder & Felder, 1860)
Pseudoscada erruca (Hewitson, 1855)
Pteronymia carlia Schaus, 1902
Sais rosalia rosalinde Weymer, 1890
Thyridia psidii cetoides (Rosenberg & Talbot, 1914)
Tithorea harmonia pseudethra Butler, 1873 x *Tithorea harmonia pseudonyma* Staudinger, 1894[a]
Heliconiinae (20)
Acraeini (7)
Actinote carycina Jordan, 1913
Actinote discrepans d'Almeida, 1958
Actinote genitrix genitrix d'Almeida, 1922**
Actinote melanisans Oberthür, 1917
Actinote pellenea pellenea Hübner, [1821]
Actinote pyrrha pyrrha (Fabricius, 1775)
Actinote sp.
Argynnini (2)
Euptoieta hegesia meridiania Stichel, 1938
Euptoieta hortensia (Blanchard, 1852)
Heliconiini (11)
Agraulis maculosa (Stichel, [1908])
Dione juno juno (Cramer, 1779)
Dione moneta moneta Hübner, [1825]
Dryadula phaetusa (Linnaeus, 1758)
Dryas alcionea (Cramer, 1779)
Eueides aliphera aliphera (Godart, 1819)
Eueides isabella dianasa (Hübner, [1806])
Heliconius besckei (Ménétriés, 1857)
Heliconius erato phyllis (Fabricius, 1775)
Heliconius ethilla polychrous Felder & Felder, 1865 x *Heliconius ethilla narcaea* (Godart, 1819)[a]
Philaethria wernickei (Röber, 1906)**
Libytheinae (1)
Libytheana carinenta carinenta (Cramer, [1777])
Limenitidinae (18)
Limenitidini (18)
Adelpha abia (Hewitson, 1850)
Adelpha calliphane Frühstorfer, 1915
Adelpha epizygis epizygis Frühstorfer, 1915
Adelpha falcipennis Frühstorfer, 1915
Adelpha gavina Frühstorfer, 1915**
Adelpha iphicleola leucates Frühstorfer, 1915

Continue...

Table 2. Continuation

Adelpha iphiclus iphiclus (Linnaeus, 1758)**
Adelpha lycorias lycorias (Godart, [1824])
Adelpha malea goyama Schaus, 1902
Adelpha melona pseudarete Frühstorfer, 1915
Adelpha mythra (Godart, [1824])
Adelpha plesaure phliassa (Godart, [1824])
Adelpha serpa serpa (Boisduval, [1836])
Adelpha syma (Godart, [1824])
Adelpha thesprotia (Felder & Felder, [1867])
Adelpha thessalia indefecta Frühstorfer, 1913
Adelpha thoasa gerona (Hewitson, 1867)
Adelpha zea (Hewitson, 1850)
Nymphalinae (22)
Coeini (1)
Historis odius dious Lamas, 1995^{F}
Junoniini (1)
Junonia evarete evarete (Cramer, 1779)
Melitaeini (9)
Anthanassa hermas hermas (Hewitson, 1864)
Chlosyne lacinia saundersi (Doubleday, [1847])
Eresia lansdorfi (Godart, 1819)
Ortilia dicoma (Hewitson, 1864)
Ortilia ithra (Kirby, 1900)
Ortilia orthia (Hewitson, 1864)
Ortilia velica durnfordi (Godman & Salvin, 1878)
Tegosa claudina (Eschscholtz, 1821)
Telenassa teletusa teletusa (Godart, [1824])**
Nymphalini (7)
Colobura dirce dirce (Linnaeus, 1758)^{F}
Hypanartia bella (Fabricius, 1793)
Hypanartia lethe (Fabricius, 1793)
Smyrna blomfildia blomfildia (Fabricius, 1781)^{F}
Vanessa braziliensis (Moore, 1883)
Vanessa carye (Hübner, [1812])
Vanessa myrinna (Doubleday, 1849)
Victorinini (4)
Anartia amathea roeselia (Eschscholtz, 1821)
Anartia jatrophae jatrophae (Linnaeus, 1763)
Siproeta epaphus trayja Hübner, [1823]
Siproeta stelenes meridionalis (Frühstorfer, 1909)
Satyrinae (68)
Brassolini (17)
Blepolenis batea batea (Hübner, [1821])^{F}
Brassolis sophorae vulpeculus Stichel, 1902
Caligo beltrao (Illiger, 1801)^{F}
Caligo illioneus pampeiro Frühstorfer, 1904^{F}
Catoblepia amphirhoe (Hübner, [1825])**^{F}
Catoblepia berecynthia unditaenia (Frühstorfer, 1907)^{F}
Dynastor darius ictericus Stichel, 1904
Eryphanis automedon automedon (Cramer, [1775])^{F}
Eryphanis reevesii reevesii (Doubleday, [1849])^{F}
Narope cyllarus Westwood, 1851**^{F}
Narope cyllastros Doubleday, [1849]^{F}
Narope panniculus Stichel, 1904^{F}
Opoptera aorsa aorsa (Godart, [1824])^{F}
Opsiphanes cassiae crameri Felder & Felder, 1862^{F}
Opsiphanes invirae remoliatus Frühstorfer, 1907^{F}
Opsiphanes quiteria meridionalis Staudinger, 1887^{F}
Selenophanes cassiope guarany Casagrande, 1992^{F}
Melanitini (1)
Manataria hercyna hercyna (Hübner, [1821])^{F}
Morphini (6)
Antirrhea archaea Hübner, [1822]^{F}
Morpho aega (Hübner, [1822])^{F}
Morpho anaxibia (Esper, [1801])^{F}
Morpho epistrophus titei (Le Moult & Réal, 1962)^{F}
Morpho helenor achillides Felder & Felder, 1867^{F}
Morpho portis thamyris (Felder & Felder, 1867)**^{F}
Satyrini (44)
Amphidecta pignerator simplicia Weymer, 1910^{F}
Amphidecta reynoldsi Sharpe, 1890^{F}
Argentaria hygina (Butler, 1877)^{F}
Argentaria libitina (Butler, 1870)^{F}
Argentaria pagyris (Godart, [1824])^{F}
Caeruleuptychia helena (Anken, 1994)**^{F}
Capronnieria galesus (Godart, [1824])^{F}
Carminda griseldis (Weymer, 1911)^{F}
Carminda paeon (Godart, [1824])^{F}
Cisandina lea (Cramer, 1777)^{F}
Cissia eous (Butler, 1867)^{F}
Cissia phronius (Godart, [1824])^{F}
Deltaya ocypete (Fabricius, 1776)^{F}
Deltaya pallema (Schaus, 1902)^{F}
Deltaya sp. n.#^{F}
Eteona tisiphone (Boisduval, [1836])^{F}
Forsterinaria necys (Godart, [1824])^{F}
Forsterinaria quantius (Godart, [1824])^{F}
Godartiana muscosa (Butler, 1870)^{F}
Hermeuptychia atalanta (Butler, 1867)^{F}
Hermeuptychia gisella (Hayward, 1957)^{F}
Malaveria affinis (Butler, 1867)^{F}
Malaveria grimon (Godart, [1824])**^{F}
Malaveria mimula (Hayward, 1954)^{F}
Modestia sylvina (Felder & Felder, 1867)^{F}
Moneuptychia castrensis (Schaus, 1902)^{F}
Moneuptychia soter (Butler, 1877)^{F}
Pareuptychia ocirrhoe interjecta (d'Almeida, 1952)^{F}
Paryphthimoides poltys poltys (Prittwitz, 1865)^{F}
Paryphthimoides terrestris grevei Zacca, Casagrande & Mielke 2020
"Pharneuptychia" innocentia (Felder & Felder, 1867)**^{F}
Posttaygetis penelea (Cramer, [1777])^{F}
Praepedaliodes phanias (Hewitson, 1862)^{F}
Pseudodebis euptychidia (Butler, 1868)^{F}
Taguaiba ypthima (Hübner, [1821])^{F}
Taygetina kerea (Butler, 1869)^{F}
Taygetis acuta Weymer, 1910**^{F}
Taygetis laches (Fabricius, 1793)^{F}

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Table 2. Continuation

Taygetis rufomarginata rufomarginata Staudinger, 1888[F]
Taygetis tripunctata Weymer, 1907[F]
Yphthimoides celmis (Godart, [1824])[F]
Yphthimoides ordinaria Freitas, Kaminski & Mielke, 2012[F]
Yphthimoides yphthima (Felder & Felder, [1867])[F]
Zischkaia pacarus (Godart, [1824])[F]
PIERIDAE (24)
Coliadinae (14)
Anteos clorinde (Godart, [1824])
Anteos menippe (Godart, [1818])
Eurema albula sinoe (Godart, 1819)
Eurema deva deva (Doubleday, 1847)
Eurema elathea flavescens (Chavannes, 1850)
Phoebis argante argante (Fabricius, 1775)
Phoebis marcellina (Cramer, [1779])
Phoebis neocypris neocypris (Hübner, [1823])
Phoebis philea philea (Linnaeus, 1763)
Phoebis statira statira (Cramer, [1777])
Phoebis trite banksi (Breyer, 1939)
Phoebis wallacei wallacei (Felder & Felder, 1862)
Pyrisitia leuce leuce (Boisduval, 1836)
Pyrisitia nise tenella (Boisduval, 1836)
Dismorphiinae (5)
Dismorphia amphione astynome (Dalman, 1823)
Dismorphia astyocha Hübner, [1831]
Dismorphia thermesia thermesia (Godart, 1819)
Enantia lina psamathe (Fabricius, 1793)
Pseudopieris nehemia nehemia (Boisduval, 1836)
Pierinae (5)
Pierini (5)
Ascia monuste orseis (Godart, 1819) x *Ascia monuste automate* (Burmeister, 1878)[a]
Glutophrissa drusilla drusilla (Cramer, 1777)
Itaballia demophile ssp.*
Leptophobia aripa balidia (Boisduval, 1836)
Melete lycimnia paulista Frühstorfer, 1908
HESPERIIDAE (339)
Eudaminae (68)
Entheini (1)
Phanus australis Miller, 1965
Phocidini (11)
Bungalotis astylos (Cramer, 1780)
Bungalotis midas (Cramer, 1775)
Dyscophellus damias (Plötz, 1882)**
Nascus broteas (Cramer, 1780)
Nascus paulliniae (Sepp, [1842])
Nascus phocus (Cramer, [1777])
Phocides charon (Felder & Felder, 1859)
Phocides metrodorus metron Evans, 1952**
Phocides pigmalion hewitsonius (Mabille, 1883)
Phocides polybius phanias (Burmeister, 1880)
Phocides thermus valgus (Mabille, 1883)
Eudamini (54)
Aguna asander asander (Hewitson, 1867)

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Table 2. Continuation

Aguna glaphyrus (Mabille, 1888)
Aguna megaeles megaeles (Mabille, 1888)
Aguna metophis (Latreille, [1824])
Aguna squamalba Austin & Mielke, 1998
Astraptes aulus (Plötz, 1881)
Astraptes enotrus (Stoll, [1781])
Astraptes janeira (Schaus, 1902)
Autochton neis (Geyer, 1832)*
Autochton reflexus (Mabille & Boullet, 1912)
Cecropterus dorantes (Stoll, [1790])
Cecropterus doryssus albicuspis (Herrich-Schäffer, 1869)
Cecropterus rica (Evans, 1952)
Cecropterus virescens (Mabille, 1877)
Cecropterus zarex (Hübner, 1818)
Cephise cephise (Herrich-Schäffer, 1869)
Chioides catillus catillus (Cramer, 1779)
Codatractus aminias (Hewitson, 1867)
Ectomis caunus (Herrich-Schäffer, 1869)
Ectomis octomaculata (Sepp, [1844])
Ectomis perniciosus (Herrich-Schäffer, 1869)
Epargyreus clavicornis clavicornis (Herrich-Schäffer, 1869)
Epargyreus exadeus (Cramer, [1780])
Epargyreus pseudexadeus Westwood, 1852
Epargyreus socus socus (Hübner, [1825])
Narcosius parisi (Williams, 1927)
Polygonus leo pallida Röber, 1925
Polygonus savigny savigny (Latreille, [1824])
Proteides mercurius mercurius (Fabricius, 1787)
Spathilepia clonius (Cramer, 1775)
Spicauda procne (Plötz, 1880)
Spicauda simplicius (Stoll, [1790])
Spicauda teleus (Hübner, 1821)
Telegonus alardus alardus (Stoll, 1790)
Telegonus anaphus anaphus (Cramer, [1777])
Telegonus chalco (Hübner, 1823)
Telegonus cretatus adoba (Evans, 1952)
Telegonus creteus siges (Mabille, 1903)
Telegonus elorus (Hewitson, 1867)**
Telegonus fulgor (Hayward, 1939)
Telegonus sp.
Telegonus talus (Cramer, [1777])
Telemiades aff. *squanda* Evans, 1953
Telemiades amphion (Geyer, 1832)
Telemiades antiope (Plötz, 1882)
Telemiades atlantiope Siewert, Mielke & Casagrande 2020
Telemiades brazus Bell, 1949
Telemiades laogonus (Hewitson, 1876)
Telemiades marpesus (Hewitson, 1876)
Urbanus esma Evans, 1952**
Urbanus esmeraldus (Butler, 1877)
Urbanus esta Evans, 1952
Urbanus pronta Evans, 1952
Urbanus proteus proteus (Linnaeus, 1758)

Continue...

Table 2. Continuation

Oileidini (2)
Cogia calchas (Herrich-Schäffer, 1869)
Cogia undulatus (Hewitson, 1867)
Tagiadinae (1)
Celaenorrhinini (1)
Celaenorrhinus similis Hayward, 1933
Hesperiinae (187)
Pericharini (8)
Lycas argentea (Hewitson, [1866])
Orses cynisca (Swainson, [1821])
Oz ozias (Hewitson, 1878)
Perichares adela (Hewitson, 1867)
Perichares aurina Evans, 1955
Perichares lotus (Butler, 1870)
Perichares metallica (Riley, 1921)
Perichares seneca seneca (Latreille, [1824])
Hesperiini (179)
Adlerodea mineira Mielke, 1968**
Adlerodea modesta Hayward, 1940
Adlerodea petrovna (Schaus, 1902)
Adlerodea subpunctata subpunctata (Hayward, 1940)
Aides duma duma Evans, 1955
Alerema simplex (Bell, 1930)
Anatrytone perfida (Möschler, 1879)
Anthoptus epictetus (Fabricius, 1793)
Anthoptus insignis (Plötz, 1882)**
Apaustus gracilis ssp. n.#
Artines aepitus (Geyer, [1832])
Artines aquilina (Plötz, 1882)
Artines liege Medeiros, Mielke & Casagrande 2019
Artonia artona (Hewitson, 1868)
Callimormus diaeses Schaus, 1902**
Callimormus rivera (Plötz, 1882)**
Callimormus saturnus (Herrich-Schäffer, 1869)
Callimormus simplicius Hayward, 1939**
Calpodes esperi esperi (Evans, 1955)
Calpodes ethlius (Stoll, [1782])
Calpodes longirostris (Sepp, [1840])
Calpodes saladin catha (Evans, 1955)**
Calpodes salius (Cramer, [1775])
Cantha roraimae (Bell, 1932)
Carystoides basoches (Latreille, [1824])
Carystus hylaspes (Stoll, 1781)
Carystus lota (Hewitson, 1877)
Cobalopsis catocala (Herrich-Schäffer, 1869)
Cobalopsis cocalus (Hayward, 1939)
Cobalopsis nero (Herrich-Schäffer, 1869)
Cobalopsis obscurior (Hayward, 1934)
Cobalopsis valerius (Möschler, 1879)
Cobalus virbius virbius (Cramer, [1777])
Conga chydaea (Butler, 1877)
Conga iheringii (Mabille, 1891)
Contrastia distigma (Plötz, 1882)**
Corticea corticea (Plötz, 1882)
Corticea lysias potex Evans, 1955
Corticea sp.**
Cumbre meridionalis (Hayward, 1934)
Cyclosma altama (Schaus, 1902)
Cymaenes alumna (Butler, 1877)
Cymaenes cavalla Evans, 1955
Cymaenes gisca Evans, 1955
Cymaenes lepta (Hayward, 1939)
Cymaenes loxa Evans, 1955
Cymaenes tripunctata (Latreille, [1824])
Cynea bistrigula (Herrich-Schäffer, 1869)
Cynea cannae (Herrich-Schäffer, 1869)
Cynea diluta (Herrich-Schäffer, 1869)
Cynea irma (Möschler, 1879)
Cynea melius (Geyer, 1832)
Damas clavus (Herrich-Schäffer, 1869)
Decinea dama (Herrich-Schäffer, 1869)
Decinea denta pruda Evans, 1955
Dion uza uza (Hewitson, 1877)
Ebusus ebusus ebusus (Cramer, [1780])
Eprius obrepta (Kivirikko, 1936)
Eprius repens Evans, 1955
Euphyes leptosema (Mabille, 1891)
Euphyes subferrugineus subferrugineus (Hayward, 1934)
Eutocus vetulus matildae (Hayward, 1941)
Eutus mubevensis (Bell, 1932)
Eutychide olympia (Plötz, 1882)
Eutychide physcella (Hewitson, [1866])
Evansiella cordela (Plötz, 1882)
Gallio carasta (Schaus, 1902)
Gufa fusca (Hayward, 1940)
Haza hazarma (Hewitson, 1877)
Hedone vibex catilina (Plötz, 1886)
Hylephila phyleus phyleus (Drury, [1773])
Koria kora (Hewitson, 1877)
Lamponia elegantula (Herrich-Schäffer, 1869)
Lento krexoides (Hayward, 1940)
Lerema compta (Butler, 1877)
Lerema geisa (Möschler, 1879)
Lerodea eufala eufala (W. H. Edwards, 1869)
Lucida lucia (Capronnier, 1874)
Methionopsis cinnamomea (Herrich-Schäffer, 1869)
Methionopsis ina (Plötz, 1882)
Metrocles dejongi (Austin, 2008)
Metrocles hyboma (Plötz, 1886)
Metrocles sp.
Metron noctis (Kaye, 1914)
Metron oropa (Hewitson, 1877)
Mnaseas inca Bell, 1930
Mnasicles hicetaon Godman, [1901]**
Mnasicles remus (Fabricius, 1798)
Mnasitheus gemignanii (Hayward, 1940)
Mnasitheus submetallescens (Hayward, 1940)
Mnasitheus sucova (Schaus, 1902)**

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Table 2. Continuation

Mnestheus silvaticus Hayward, 1940**
Moeris striga (Geyer, 1832)
Mucia zygia (Plötz, 1886)
Naevolus orius (Mabille, 1883)
Nastra celeus vetus (Mielke, 1969)
Neoxeniades scipio scipio (Fabricius, 1793)
Niconiades caeso (Mabille, 1891)
Niconiades linga Evans, 1955**
Niconiades merenda (Mabille, 1878)
Niconiades nikko Hayward, 1948**
Niconiades xanthaphes Hübner, [1821]
Nyctelius nyctelius nyctelius (Latreille, [1824])
Oligoria aff. *locutia* (Hewitson, 1876)
Oligoria aff. *percosius* (Godman, 1900)
Oligoria lucifer (Hübner, [1831])
Onophas columbaria distigma (Bell, 1930)
Orthos hyalinus (Bell, 1930)
Oxynthes corusca (Herrich-Schäffer, 1869)
Panoquina fusina viola Evans, 1955
Panoquina hecebolus (Scudder, 1872)
Panoquina lucas lucas (Fabricius, 1793)
Panoquina ocola ocola (Edwards, 1863)
Papias phainis Godman, 1900
Paracarystus evansi Hayward, 1938
Paracarystus hypargyra (Herrich-Schäffer, 1869)
Parphorus decora (Herrich-Schäffer, 1869)
Parphorus pseudecorus (Hayward, 1934)
Peba verames (Schaus, 1902)
Phemiades pohli pohli (Bell, 1932)
Pheraeus fastus (Hayward, 1939)
Pheraeus perpulcher (Hayward, 1934)
Phlebodes fuldai (Bell, 1930)
Polites premnas (Wallengren, 1860)
Pompeius amblyspila (Mabille, 1897)
Pompeius pompeius (Latreille, [1824])
Propapias sipariana (Kaye, 1925)
Psoralis arva (Evans, 1955)
Psoralis stacara (Schaus, 1902)
Psoralis umbrata (Erschoff, 1876)
Pyrrhopygopsis socrates socrates (Ménétriés, 1855)
Quasimellana eulogius (Plötz, 1882)
Quasimellana meridiani (Hayward, 1934)
Saturnus reticulata reticulata (Plötz, 1883) x *Saturnus reticulata conspicuus* (Bell, 1941)^{c}
Saturnus saturnus saturnus (Fabricius, 1787)
Sodalia coler (Schaus, 1902)
Sodalia dimassa (Hewitson, 1876)
Sodalia sodalis (Butler, 1877)**
Synapte aff. *silius* (Latreille, [1824])
Synapte malitiosa antistia (Plötz, 1882)
Talides riosa Evans, 1955
Thargella caura occulta (Schaus, 1902)
Thargella evansi Biezanko & Mielke, 1973
Thespieus aspernatus Draudt, 1923
Thespieus dalman (Latreille, [1824])
Thespieus ethemides (Burmeister, 1878)
Thespieus lutetia (Hewitson, [1866])**
Thespieus xarippe xarippe (Butler, 1870)
Thracides cleanthes cleanthes (Latreille, [1824])
Tigasis arita (Schaus, 1902)
Tigasis perloides (Plötz, 1882)
Tigasis serra (Evans, 1955)
Tirynthia conflua (Herrich-Schäffer, 1869)
Tirynthoides virilis (Riley, 1929)
Tisias lesueur lesueur (Latreille, [1824])** x *Tisias lesueur canna* Evans, 1955^{c}
Tricrista roppai (Mielke, 1980)**
Troyus diversa diversa (Herrich-Schäffer, 1869)
Troyus phyllides (Röber, 1925)
Turesis complanula (Herrich-Schäffer, 1869)
Vacerra bonfilius bonfilius (Latreille, [1824])
Vacerra caniola elva Evans, 1955
Vacerra evansi Hayward, 1938
Vehilius inca (Scudder, 1872)
Vehilius stictomenes stictomenes (Butler, 1877)
Vettius phyllus prona Evans, 1955**
Vidius similis Mielke, 1980
Vidius vidius (Mabille, 1891)
Vinius letis (Plötz, 1883)**
Vinius pulcherrimus Hayward, 1934
Vinius tryhana istria Evans, 1955
Virga austrinus (Hayward, 1934)
Virga silvanus (Hayward, 1947)
Vistigma bryanti (Weeks, 1906)
Vistigma xanthobasis (Hayward, 1939)
Xeniades chalestra corna Evans, 1955
Xeniades orchamus (Cramer, [1777])
Zariaspes mys (Hübner, [1808])
Zenis jebus jebus (Plötz, 1882)
Zenis minos (Latreille, [1824])**
Heteropterinae (1)
Heteropterini (1)
Dalla diraspes (Hewitson, 1877)
Pyrginae (62)
Achlyodini (10)
Achlyodes busirus rioja Evans, 1953
Aethilla echina coracina Butler, 1870
Eantis thraso (Hübner, [1807])
Milanion leucaspis (Mabille, 1878)
Ouleus fridericus riona Evans, 1953
Pythonides lancea (Hewitson, 1868)
Quadrus cerialis (Stoll, [1782])
Quadrus u-lucida mimus (Mabille & Boullet, 1917)
Zera hyacinthinus servius (Plötz, 1884)
Zera tetrastigma erisichthon (Plötz, 1884)
Carcharodini (20)
Bolla atahuallpai (Lindsey, 1925)
Bolla catharina (Bell, 1937)**

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Table 2. Continuation

Gorgopas petale (Mabille, 1888)
Incisus incisus (Mabille, 1878)
Nisoniades bipuncta (Schaus, 1902)
Nisoniades castolus (Hewitson, 1878)
Nisoniades macarius (Herrich-Schäffer, 1870)
Nisoniades maura (Mabille & Boullet, 1917)
Pachyneuria inops (Mabille, 1877)
Pellicia costimacula costimacula Herrich-Schäffer, 1870
Pellicia dimidiata zamia Plötz, 1882**
Pellicia ranta rancida Evans, 1953**
Perus minor (Schaus, 1902)
Polyctor polyctor polyctor (Prittwitz, 1868)
Staphylus ascalon (Staudinger, 1876)
Staphylus chlorocephala (Latreille, [1824])
Staphylus insignis Mielke, 1980
Staphylus melangon melangon (Mabille, 1883)
Viola minor (Hayward, 1933)
Xispia satyrus (Jörgensen, 1935)
Erynnini (16)
Camptopleura auxo (Möschler, 1879)
Chiomara mithrax (Möschler, 1879)
Chiothion asychis autander (Mabille, 1891)
Cycloglypha thrasibulus thrasibulus (Fabricius, 1793)
Ebrietas anacreon anacreon (Staudinger, 1876)
Echelatus sempiternus simplicior (Möschler, 1877)
Festivia cronion (Felder & Felder, 1867)
Gesta gesta (Herrich-Schäffer, 1863)
Gorgythion begga begga (Prittwitz, 1868)
Gorgythion beggina escalophoides Evans, 1953
Grais stigmaticus stigmaticus (Mabille, 1883)
Helias phalaenoides palpalis (Latreille, [1824])
Hoodus pelopidas (Fabricius, 1793)
Mylon maimon (Fabricius, 1775)
Sostrata bifasciata bifasciata (Ménétriés, 1829)
Timochares trifasciata trifasciata (Hewitson, 1868)
Pyrgini (16)
Anisochoria sublimbata Mabille, 1883
Antigonus erosus (Hübner, [1812])
Antigonus nearchus (Latreille, [1817])
Burnsius orcus (Stoll, [1780])
Burnsius orcynoides (Giacomelli, 1928)
Canesia canescens pallida (Röber, 1925)
Heliopetes alana (Reakirt, 1868)
Heliopetes arsalte (Linnaeus, 1758)
Heliopetes libra Evans, 1944
Heliopetes ochroleuca Zikán, 1938
Heliopetes omrina (Butler, 1870)
Heliopetes petrus (Hübner, [1819])**
Paches liborius areta (Evans, 1953)
Spioniades artemides (Stoll, [1782])
Trina geometrina geometrina (Felder & Felder, [1867])
Xenophanes tryxus (Stoll, [1780])
Pyrrhopyginae (20)
Zoniini (1)
Zonia zonia diabo Mielke & Casagrande, 1998**
Passovini (6)
Agara epimachia edix (Evans, 1951)
Agara pardalina yacutinga (Mielke & Casagrande, 2011)
Granila paseas (Hewitson, 1857)**
Myscelus epigona Herrich-Schäffer, 1869
Passova passova practa Evans, 1951
Passova polemon (Hopffer, 1874)
Pyrrhopygini (13)
Blubella adonis (Bell, 1931)
Blubella azeta giffordi (Mielke, 1995)
Elbella intersecta losca Evans, 1951
Elbella lamprus lamprus (Hopffer, 1874)
Elbella viriditas viriditas (Skinner, 1920)#
Jematus gnetus brevipennis (Schaus, 1902)
Mysoria barcastus barta Evans, 1951
Ochropyge ruficauda (Hayward, 1932)**
Parelbella ahira extrema (Röber, 1925)
Pyrrhopyge attis subnubilus Hayward, 1935
Pyrrhopyge charybdis charybdis Westwood, 1852**
Pyrrhopyge pelota Plötz, 1879**
Santea antias (Felder & Felder, 1859)**
HEDYLIDAE (1)
Hedylinae (1)
Macrosoma zikani (Prout, 1932)**

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et al. 2014, Busby et al. 2017, Hall 2018) are *Sais rosalia rosalinde* Weymer, 1890 (Nymphalidae), *Paraspiculatus orobia* (Hewitson, 1867) (Lycaenidae), and *Pseudolivendula h. hemileuca* (Bates, 1868) (Riodinidae). Among those typical from Cerrado (Mielke et al. 2008, Pinheiro et al. 2010, Freitas et al. 2021a) are *Aguna squamalba* Austin & Mielke, 1998, *Blubella azeta giffordi* (Mielke, 1995)*,* *Elbella intersecta losca* (Evans, 1951), *Staphylus melangon epicaste* Mabile, 1903 (Hesperiidae), *Amphidecta reynoldsi* Sharpe, 1890, *Brevioleria seba emyra* (Haensch, 1905), *Callicore s. sorana* (Godart, [1824]), *Fountainea glycerium cratais* (Hewitson, 1874), *Malaveria mimula* (Hayward, 1954), *Paryphthimoides p. poltys* (Prittwitz, 1865), *"Pharneuptychia" innocentia* (Felder & Felder, 1867), *Yphthimoides celmis* (Godart, [1824]) (Nymphalidae), *Symbiopsis lenitas* (Druce, 1907) (Lycaenidae), and *Rhetus periander arthuriana* (Sharpe, 1890) (Riodinidae).

The records of six species at Iguaçu NP represent the southernmost point of their respective previously documented distributions. These are: 1) *Camissecla vesper* (Druce, 1909), 2) *Ipidecla crepundia* (Druce, 1909), 3) *Nesiostrymon tristis* (Lathy, 1926) (Lycaenidae), 4) *Joiceya praeclarus* Talbot, 1928 (for more details see Greve et al. 2013), 5) *Theope p. pakitza* Hall & Harvey, 1998 (Riodinidae), and 6) *Eunica m. malvina* Bates, 1864 (Nymphalidae).

Among the sampled taxa, six were recorded for the first time in Brazil (Figure 4), namely: 1) *Apaustus gracilis* ssp. n., 2) *Elbella v. viriditas* (Skinner, 1920) (Hesperiidae), 3) *Deltaya* sp. n. (Nymphalidae), 4) *Symbiopsis* sp. n. (Lycaenidae), 5) *Emesis orichalceus* Stichel, 1916 and 6) *Theope p. pakitza* (Riodinidae). The new taxa of *Apaustus*, *Deltaya* and *Symbopsis* were discovered in this study.

Figure 3. Sample of representative species present at Iguaçu National Park and surrounding areas representing six butterfly families (only Hedylidae is not illustrated): A) *Pyrrhopygopsis s. socrates* (Ménétriés, 1855); B) *Dalla diraspes* (Hewitson, 1877); C) *Festivia cronion* (Felder & Felder, 1867); D) *Mysoria barcastus barta* Evans, 1951 (Hesperiidae); E) *Myscelia orsis* (Drury, [1782]); F) *Epityches eupompe* (Geyer, [1832]); G) *Argentaria libitina* (Butler, 1870); H) *Catagramma pygas thamyras* Ménétriés, 1857 (Nymphalidae); I) *Zizula cyna* (Edwards, 1881); J) *Cyanophrys herodotus* (Fabricius, 1793); K) *Heterosmaitia palegon* (Cramer, [1780]); L) *Evenus regalis* (Cramer, [1775]) (Lycaenidae); M) *Rhetus periander arthuriana* (Sharpe, 1890); N) *Alesa prema* (Godart, [1824]); O) *Caria p. plutargus* (Fabricius, 1793); P) *Ariconias glaphyra* (Westwood, 1851) (Riodinidae); Q) *Anteos clorinde* (Godart, [1824]); R) *Pyrisitia l. leuce* (Boisduval, 1836); S) *Itaballia demophile* ssp.; T) *Dismorphia amphione astynome* (Dalman, 1823) (Pieridae); U) *Heraclides hectorides* (Esper, 1794); V) *Protesilaus stenodesmus* (Rothschild & Jordan, 1906); W) *Mimoides protodamas* (Godart, 1819); X) *Parides agavus* (Drury, 1782) (Papilionidae).

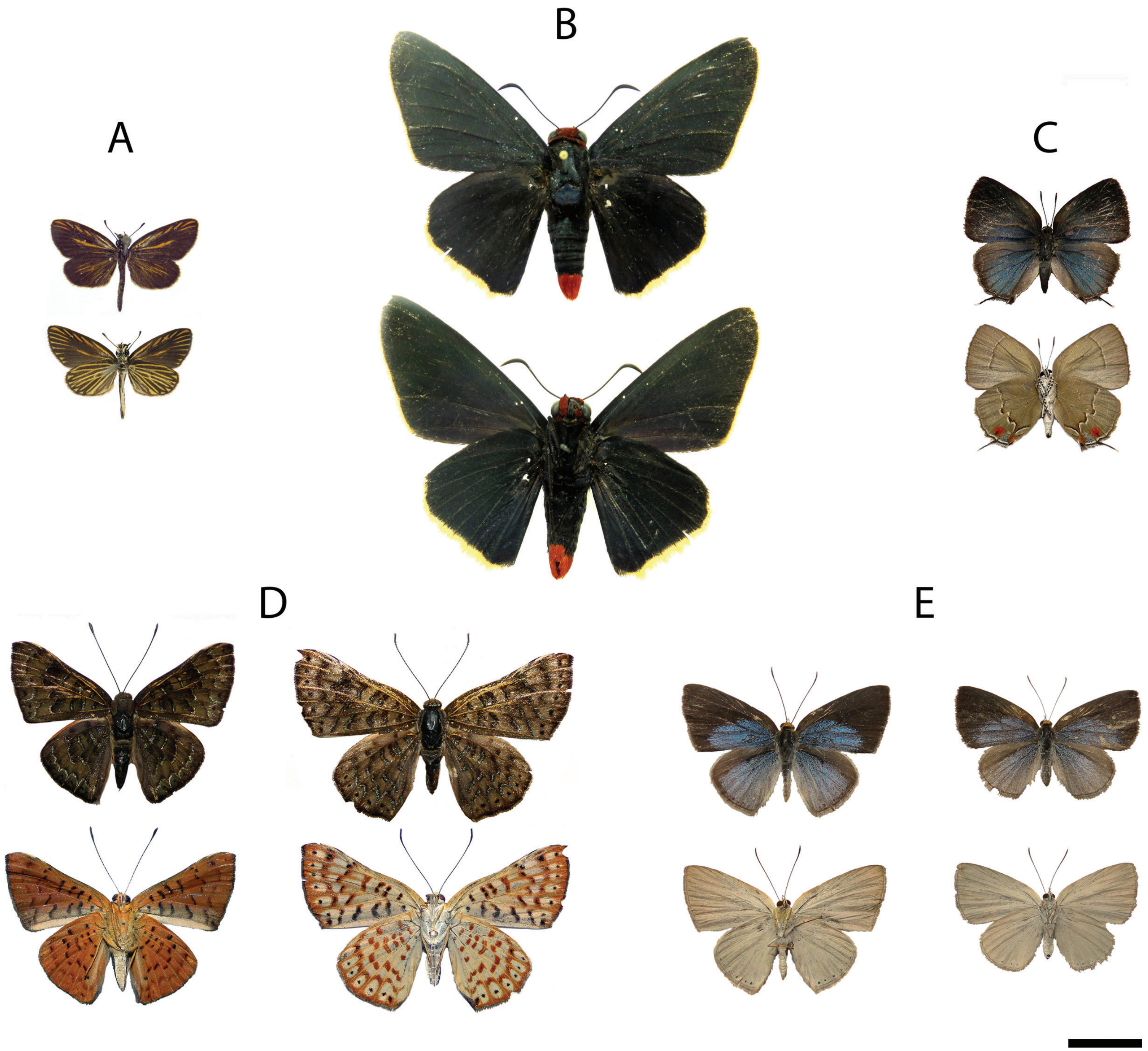

Figure 4. Taxa recorded for the first time in Brazil (except for the undescribed species of *Deltaya*): A) an undescribed subspecies of *Apaustus gracilis*, male; B) *Elbella v. viriditas* (Skinner, 1920), female (Hesperiidae); C) an undescribed species of *Symbiopsis*, female (Lycaenidae); D) *Emesis orichalceus* Stichel, 1916, male (left) and female (right); E) *Theope p. pakitza* Hall & Harvey, 1998, male (left) and hitherto unknown female (right) (Riodinidae). Scale bar = 1 cm.

Six taxa were included in at least one endangered faunal list (Mielke & Casagrande 2004, ICMBio 2018a): 1) *Zonia zonia diabo* Mielke & Casagrande, 1998, 2) *Ochropyge ruficauda* (Hayward, 1932), 3) *Passova passova practa* Evans, 1951 (Hesperiidae), 4) *Narope cyllarus* Westwood, 1851 (Nymphalidae), 5) *Alesa prema* (Godart, [1824]), and 6) *Joiceya praeclarus* (Riodinidae).

Discussion

1. Species richness

The 787 species recorded at Iguaçu NP and its surrounding areas represent 22.2% of the 3549 butterfly species known in Brazil (Casagrande & Duarte 2022). Except for the family Hedylidae, which was not included in previous Papilionoidea inventories in the Atlantic Forest, the other 786 species make Iguaçu NP the richest known site in butterfly species among areas with Semideciduous Forest. The park is also among the three richest sites in butterfly species of Atlantic Forest domain, together with the municipality of Linhares, in the state of Espírito Santo (835 species) (Brown Jr. & Freitas 2000), and Itatiaia National Park, in the states of Rio de Janeiro and Minas Gerais (914 species) (Zikán & Zikán 1968).

Among the records that may be added in the future to Iguaçu NP are the taxa that have been recorded exclusively at Iguazú National Park (hereafter Iguazú NP), Yacutinga Private Reserve (hereafter Yacutinga PR) and Surucuá Private Reserve (hereafter Surucuá PR),

Table 3. Species that are likely to occur in Iguaçu NP and may be included in future lists, based on records from neighboring protected areas in Argentina (Iguazú NP, Yacutinga PR and Surucuá PR) (Núñez-Bustos 2008, 2009, 2019, Klimaitis et al. 2018, Núñez-Bustos & Penco 2020, Rosa et al. 2021, Núñez-Bustos in preparation). Species richness for each family are provided within parenthesis.

Family	Species
Papilionidae (1)	*Protesilaus telesilaus vitellus* (Frühstorfer, 1907)
Lycaenidae (9)	*Contrafacia imma* (Prittwitz, 1865)
	Cyanophrys bertha (Jones, 1912)
	Kolana sp. n.
	Ministrymon una (Hewitson, 1873)
	Nicolaea cupa (Druce, 1907)
	Nicolaea opaliana (Hayward, 1967)
	Olynthus ophelia (Hewitson, 1867)
	Paraspiculatus hannelore (Bálint & Moser, 2001)
	Strephonota dindymus (Cramer, 1775) (cited as *Strephonota sphinx* (Fabricius, 1775))
Riodinidae (8)	*Baeotis hisbon* (Cramer, 1775)
	Chadia cadytis (Hewitson, 1866)
	Emesis fatimella fatimella Westwood, 1851
	Eurybia misellivestis Stichel, 1910
	Exoplisia aphanis (Stichel, 1910)
	Ithomiola orpheus (Westwood, 1851)
	Melanis smithiae smithiae (Westwood, 1851)
	Theope cmielkei Jauffret & Jauffret, 2009
Nymphalidae (15)	*Actinote brylla* Oberthür, 1917
	Adelpha cytherea aea (Felder & Felder, 1867)
	Caligo martia (Godart, [1824])
	Heterosais edessa (Hewitson, [1855])
	Ithomia drymo Hübner, 1816
	Memphis appias (Hübner, [1825])
	Memphis otrere (Hübner, [1825])
	Morpho hercules diadema Frühstorfer, 1905
	Morpho menelaus coeruleus (Perry, 1810)
	Penetes pamphanis Doubleday, [1849]
	Pharneuptychia phares (Godart, [1824])
	Phystis simois variegata (Hewitson, 1864)
	Splendeuptychia ambra (Weymer, [1911])
	Splendeuptychia tupinamba Freitas, Huertas & Rosa 2021
	Taygetis virgilia (Cramer, 1776)
Pieridae (8)	*Colias lesbia lesbia* (Fabricius, 1775)
	Enantia clarissa (Weymer, 1895)
	Eurema phiale paula (Röber, 1909)
	Ganyra phaloe endeis (Godart, 1819)
	Glennia pylotis (Godart, 1819)
	Hesperocharis paranensis paranensis Schaus, 1898
	Perrhybris pamela eieidias Hübner, [1821]
	Pieriballia viardi molione (Frühstorfer, 1908)
Hesperiidae (35)	*Anatrytone mella* (Godman, 1900)
	Blubella blanda (Evans, 1951)
	Callimormus radiola pusillus Hayward, 1934
	Carystus phorcus claudianus (Latreille, [1824])
	Conga urqua (Schaus, 1902)
	Corticea noctis (Plötz, 1882)
	Cycloglypha caeruleonigra Mabille, 1903
	Cynea popla Evans, 1955
	Cynea robba nippa Evans, 1955
	Diaeus variegata (Plötz, 1884)
	Dyscophellus porcius doriscus (Hewitson, 1867)
	Ectomis orphne (Plötz, 1881)
	Epargyreus tmolis (Burmeister, 1875)
	Jember menechmus menechmus (Mabille, 1878)
	Justinia maculata (Bell, 1930)
	Libra aligula decia (Hayward, 1948)
	Lindra brasus brasus (Mielke, 1968)
	Mahotis versicolor (Latreille, [1824])
	Mimadia fallax fida (Evans, 1951)
	Nastra ethologus (Hayward, 1934)
	Nicephellus nicephorus (Hewitson, 1876)
	Nyctelius paranensis (Schaus, 1902)
	Olafia roscius roscius (Hopffer, 1874)
	Pellicia hersilia Hayward, 1939
	Pellicia najoides Hayward, 1933
	Phanes rezia (Plötz, 1882)
	Pheraeus odilia odilia (Plötz, 1884)
	Phlebodes campo campo (Bell, 1947) (misidentified as *Thoon taxes* Godman, 1900)
	Porphyrogenes vulpecula vulpecula (Plötz, 1882)
	Pseudosarbia phoenicicola Berg, 1897
	Pythonides jovianus fabricii Kirby, 1871
	Salatis salatis (Stoll, 1782)
	Staphylus melaina (Hayward, 1947)
	Staphylus musculus (Burmeister, 1875)
	Talides sergestus (Cramer, [1775])
Hedylidae (1)	*Macrosoma hedylaria* (Warren, 1894)

Continue...

Continuation

three neighboring protected areas in Argentina (Núñez-Bustos 2008, 2009, 2019, Klimaitis et al. 2018, Núñez-Bustos & Penco 2020, Núñez-Bustos in preparation). Together, these protected areas in Argentina and the Iguaçu NP in Brazil, form a practically continuous forest, composed by the same vegetal formation (except by MOF, which does not occur in the Argentinian parks), separated by the Iguaçu River. As such, it is reasonable to expect that these areas share a similar fauna. At least 77 species have been recorded only in the Argentinian parks, but all are likely to occur at Iguaçu NP. These records include 1 Papilionidae, 9 Lycaenidae, 8 Riodinidae, 15 Nymphalidae, 8 Pieridae, 35 Hesperiidae and 1 Hedylidae (Table 3), resulting in a list with 864 species of butterflies. Relevantly, D'Abrera (1987) mentioned that a tourist recorded *Prepona claudina annetta* (Gray, 1832) (at the time, *Agrias claudina claudianus* Staudinger, [1885]) in February 1987 at the Argentinian Falls, so it is possible that this species occurs in the Brazilian park as well. Among other species with possible occurrence in Iguaçu NP, we cite the Papilionidae *Pterourus cleotas* (Gray, 1832) and the Nymphalidae *Splendeuptychia tupinamba* Freitas, Huertas & Rosa 2021. *P. cleotas* has specimens deposited in DZUP/UFPR from Cascavel, a municipality with approximately the same elevation and a few kilometers from Santa Tereza do Oeste, in the Northern border of Iguaçu NP. The species *S. tupinamba* was recently described and recorded at Yacutinga PR (Misiones, Argentina) (Rosa et al. 2021).

2. *Taxonomic composition*

Brown Jr. & Freitas (2000) suggested that Nymphalidae generally represent 25% to 29% of the total species in a well-sampled inventory in the Neotropical region. At Iguaçu NP, the Nymphalidae make up 27.2% of the butterfly fauna, in full accord with predictions. Since the Nymphalidae can be satisfactorily documented with low sampling effort and their proportion in the butterfly fauna is relatively consistent, the richness of this family is an accurate surrogate for the total butterfly species richness. Alternatively, Robbins et al. (1996) suggested that Neotropical faunas consist of approximately a third Papilionidae + Pieridae + Nymphalidae (255 species at Iguaçu NP), a third Lycaenidae + Riodinidae (192 species at Iguaçu NP), and a third Hesperiidae (339 species at Iguaçu NP). This prediction was not especially accurate at Iguaçu NP. Further, even though the proportional richness of Hesperiidae greatly exceeded a third, we consider it likely that most species to be discovered in the future will belong to this family. The reason is that they are mostly inconspicuous, small-sized and fast-flying species that make them difficult to sample (Brown Jr. 1992, Brown Jr. & Freitas 1999).

At greater detail, the higher species richness of Hesperiidae (43.1%) than Nymphalidae (27.2%) is consistent in well-detailed Neotropical inventories (Brown Jr. & Freitas 2000) and may be a good indicator of "representativity" of butterfly sampling in the region (Francini et al. 2011). Furthermore, the predominance of Lycaenidae over Riodinidae is another expected pattern in butterfly assemblages in the southern Atlantic Forest (Francini et al. 2011) and seems to be related to a positive association between Riodinidae richness and local mean temperature (Brown Jr. 2005). Assemblages in northern locations of the Atlantic Forest and in the Amazon Basin, accordingly, show greater riodinid species richness.

So far, there are no long-term butterfly inventories carried out in locations in the Atlantic Forest that include Hedylidae. Thus, we do not know the representativeness of this family in the total butterfly fauna in this domain. In the Brazilian butterfly fauna, Hedylidae represents 0.6% of the total (Lourido & Duarte 2023). Assuming that the same proportion applies to the Atlantic Forest, we could expect the occurrence of up to four additional species of this family in Iguaçu NP, suggesting that it may be underrepresented in the present inventory.

By using VSR traps, 27 species of fruit-feeding nymphalids were sampled (out of a total of 112 sampled from this guild), of which four were sampled exclusively by this method: *Amphidecta pignerator simplicia* Weymer, 1910, *A. reynoldsi*, *Moneuptychia castrensis* (Schaus, 1902), and *Yphthimoides yphthima* (Felder & Felder, [1867]). In the present study, VSR traps were used in a complementary way, and despite the low sampling effort employed in this method, it was effective in recording species that were not found in the active sampling with entomological nets. This may be related to the habits of these species (Freitas et al. 2021b). For example, among the species that were sampled exclusively by traps, *A. pignerator simplicia* and *A. reynoldsi* have crepuscular habits, while *Y. yphthima* was sampled in a canopy trap.

Active searching for immature stages (especially on cold or rainy days, unfavorable for sampling adults) has also proven useful in adding species to the list. Whenever possible, the collected immatures were raised in the laboratory until the emergence of the adult for secure identification. The adults of some of these reared species were never seen in the field, such as the hesperid *Thracides c. cleanthes* (Latreille, [1824]), with eggs found on *Syagrus romanzoffiana* (Cham.) Glassman (Arecaceae); the nymphalid *Opsiphanes cassiae crameri* Felder & Felder, 1862, with a pupa found on exotic *Heliconia rostrata* Ruiz & Pav. (Heliconiaceae); the nymphalid *Dynastor darius ictericus* Stichel, 1904, whose pupa with signs of parasitoidism was found on *Ananas bracteatus* (Lindl.) Schult. & Schult.f. (Bromeliaceae); the riodinid *Napaea eucharila* (Bates, 1867), with larvae found on several Bromeliaceae species; and the riodinid *Hyphilaria thasus* (Stoll, 1780), with larvae found on several native and exotic Orchidaceae species, similar to that reported by Núñez-Bustos (2008), who raised a larva found on *Octomeria pinicola* Barb. Rodr. A remarkable case was that of the nymphalid *Selenophanes cassiope guarany* Casagrande, 1992, whose immature stages were previously unknown and could then be described (Shirai et al. 2016) after a female was observed ovipositing on leaves of *S. romanzoffiana* at dusk. Certain species may be more likely to be found in their immature stages for several reasons. Some spend most of their life cycle as immatures, especially those whose adults do not feed (e.g., Urich & Emmel 1991). Others have adults that fly mostly in the canopy or are active for a restricted time of day (DeVries 1997, Hall & Willmott 2010). *D. darius* fits into more than one of these explanations. In the adult stage, this is a crepuscular species that lives relatively little time and does not feed, which is also why it is not sampled in VSR traps. In a study conducted in the Cerrado domain (Silva et al. 2011), a survey focused on immature stages of Lycaenidae resulted in six new species records for a heavily sampled locality such as the Federal District (central Brazil), suggesting that this methodology has been underestimated in butterfly inventories.

Some taxa were only recorded above 500 meters elevation, where the montane subformation of SSF and its ecotone with MOF occur. These taxa include *Amphidecta reynoldsi*, *Archaeoprepona chalciope* (Hübner, [1823]), *Diaethria e. eluina* (Hewitson, [1855]), *Dynamine meridionalis* Röber, 1915, *Eteona tisiphone* (Boisduval, 1836), *Heliconius besckei* (Ménétriés, 1857), *Cisandina lea* (Cramer, 1777), *Morpho aega* (Hübner, [1822]), *Opoptera a. aorsa* (Godart, [1824]) (Nymphalidae), *Mimoides protodamas* (Godart, 1819), *Neographium asius* (Fabricius, 1781) (Papilionidae), *Catocyclotis malca* (Schaus, 1902), *Emesis fastidiosa* Ménétriés, 1855, *Euselasia eusepus* (Hewitson, [1853]), *Euselasia zara* (Westwood, 1851), *Rhetus periander eleusinus* Stichel, 1910 (Riodinidae), *Gorgopas petale* (Mabille, 1888), and *Thespieus x. xarippe* (Butler, 1870) (Hesperiidae). Although subspecies *R. periander eleusinus* and *R. periander arthuriana* fly together in other regions, in Iguaçu NP they were recorded separately – one individual of *R. periander eleusinus* in the highest part of the park whereas *R. periander arthuriana* was very common in low areas.

Among the recorded species, six were included in the Brazil Red Book of Threatened Species of Fauna (ICMBio 2018a) and/or in the Paraná State Red Book of Threatened Species of Fauna (Mielke & Casagrande 2004). These species are *Zonia zonia diabo*, *Ochropyge ruficauda*, *Passova passova practa* (Hesperiidae), *Narope cyllarus* (Nymphalidae), *Alesa prema* and *Joiceya praeclarus* (Riodinidae). Greve et al. (2013) suggested changing the conservation status of *J. praeclarus* to DD ("Data Deficient") due to the new record for Foz do Iguaçu during the inventory. This record increased the species geographic distribution, which was previously known only from the type locality, in Mato Grosso, Brazil. In the case of *Passova passova practa*, Dolibaina et al. (2010) suggested removing the species from the Red List of Paraná, because new records of it in the study area and the abundance of larvae on host plant suggest that the rarity of this species is an adult sampling artifact. *Z. zonia diabo* and *J. praeclarus* were recorded only in surrounding areas of Iguaçu NP, in small patches of secondary forest, which suggests that these species may be more environmentally tolerant than previously thought. However, even though these species have not yet been detected inside the Iguaçu NP, they certainly also occur there, reinforcing the importance of this protected area for its conservation, because populations that occur in small forest fragments tend to be much more unstable and subject to local extinctions by stochastic factors or anthropogenic disturbances (Brown Jr. 1992).

Six species had their known distribution significantly increased after the present study: *Camissecla vesper*, *Ipidecla crepundia*, *Nesiostrymon tristis* (Lycaenidae), *Joiceya praeclarus*, *Theope p. pakitza* (Riodinidae), and *Eunica m. malvina* (Nymphalidae). The three species of Lycaenidae had previously been recorded in Rio de Janeiro state (Duarte et al. 2010). *Theope p. pakitza* had been known only from a Peruvian male (Hall 1998), and its female is illustrated here for the first time (Figure 4E). In the case of *Eunica m. malvina*, we recorded a female in March 2016 landed on a high leaf of *Luehea divaricata* Mart. & Zucc. (Malvaceae) at the margin of the Iguaçu River. Otherwise, in the Atlantic Forest this species occurs in the states of Bahia, Espírito Santo, Rio de Janeiro, Minas Gerais and São Paulo Paulo (Jenkins 1990, Santos et al. 2018). In the case of the distributions previously documented for the riodinids *J. praeclarus* and *T. p. pakitza*, the increase was over 1000 km, showing that even in a well-studied group like butterflies, the Wallacean shortfall is still present.

Among the pairs of subspecies with sympatric distribution sampled, some produce intermediate forms, natural hybrids, such as the pairs nymphalids *Heliconius ethilla polychrous* Felder & Felder, 1865 x *H. ethilla narcaea* (Godart, 1819), *Hypothyris euclea laphria* (Doubleday, 1847) x *H. euclea nina* (Haensch, 1905), and *Tithorea harmonia pseudethra* Butler, 1873 x *T. harmonia pseudonyma* Staudinger, 1894. Such phenomenon is common where endemism zones meet, as shown by Brown Jr. (1982). However, other two pairs of subspecies, the hesperids *Saturnus reticulata reticulata* (Plötz, 1883) x *S. reticulata conspicuus* (Bell, 1941) and 8) *Tisias lesueur lesueur* (Latreille, [1824]) x *T. lesueur canna* Evans, 1955, actually correspond to distinct species (Mielke et al. in preparation). In other cases, such as the pairs riodinids *Melanis aegates albugo* (Stichel, 1910) x *M. aegates limbata* (Stichel, 1925) and *Rhetus periander arthuriana* (Sharpe, 1890) x *R. periander eleusinus* Stichel, 1910, further studies are needed to define the real status of these taxa. These pairs of sympatric subspecies recorded, as well as several taxa typical of other domains, is remarkable. Biogeographically, Iguaçu NP is situated in a transitional area between endemism zones (Brown Jr.& Mielke 1968, Brown Jr. 1982), which may help explain these findings. In addition, the riparian forest of the Paraná basin functions as an ecological corridor for species with a more northerly distribution, facilitating their dispersal to the region, which seems to be the southern limit of distribution for many butterfly species.

For those species that were only found as literature records or without vouchers, these records were not included. For example, there is a citation of *Caligo b. brasiliensis* (C. Felder, 1862) in an unpublished study, which was mentioned in a former version of the management plan of Iguaçu NP (IBAMA 1999), but the species was not listed in the present study because the voucher specimen was not located. Also, all records for this species from iNaturalist were rejected because the available pictures did not correspond to natural observations in Foz do Iguaçu, but to individuals raised in captivity in the butterfly center of "Parque das Aves", a private institution neighboring Iguaçu NP. Furthermore, the record of *Taygetis virgilia* (Cramer, 1776) (Nymphalidae) cited in IBAMA (1999) was rejected because the voucher specimen could not be located at DZUP. However, there are records for this species in Iguazú National Park (Misiones, Argentina) (Núñez-Bustos 2009), so it is likely that future studies may record it in the Brazilian Park as well. Finally, four species of fruit-feeding nymphalids reported in Graciotim & Morais (2016) were also not included, because: 1) the records of *Taygetis sylvia* Bates, 1866 and *Yphthimoides ochracea* (Butler, 1867) are possible misidentifications; and 2) based on nomenclatural updates (Espeland et al. 2023), *Hermeuptychia hermes* (Fabricius, 1775) and *H. fallax* (Felder & Felder, 1862) probably refer to *H. atalanta* (Butler, 1867) and *H. gisella* (Hayward, 1957), respectively.

Conclusion

Iguaçu NP and surrounding areas exhibit a heterogenous butterfly fauna with elements from different regions. Its species richness is high for a subtropical zone distant from the coast. Besides the three undescribed taxa recorded in this study, the number of other taxa originally described from specimens collected in the region, both in the Brazilian and Argentinian parks, is remarkable. Some examples are *Ochropyge ruficauda*, *Atlides misma* D'Abrera, 1995, *Caeruleuptychia helena* (Anken, 1994), and *Agara pardalina yacutinga* (Mielke & Casagrande, 2011). Furthermore, several unexpected records suggest that Iguaçu NP is a fertile field for new findings, such as the rediscoveries of *Joiceya praeclarus* and *T. p. pakitza*. The new records of these species represent a significant expansion in their geographic distributions, since *J. praeclarus* was known only from state of Mato Grosso in Brazil (over 1000 km) and had not been observed for 80 years, while *T. p. pakitza* was known only from Manú National Park in Peru (over 2000 km).

We recommend that future studies focus sampling efforts in MOF areas and their ecotone with SSF, which are the most preserved and least explored areas due to difficult accessibility. Considering the groups with high potential to represent new records for the park and its surroundings, we suggest that further studies aim at extensive collections using VSR traps for fruit-feeding Nymphalidae, the Ahrenholz technique for Hesperiidae, and light traps for mostly nocturnal Hedylidae. Due to the seasonality and short flight period of adults of certain species, some univoltine, these samplings must cover all months of the year, including during winter, in order to increase the chance of their detection.

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Author Contributions

Roberto R. Greve: substantial contribution in the concept and design of the study, contribution to data collection, contribution to data analysis and interpretation, and contribution to manuscript preparation.

Eduardo Carneiro: contribution to data collection, contribution to data analysis and interpretation, and contribution to critical revision, adding intellectual content.

Olaf H.H. Mielke: contribution to data collection, contribution to data analysis and interpretation, and contribution to critical revision, adding intellectual content.

Robert K. Robbins: contribution to data analysis and interpretation, and contribution to critical revision, adding intellectual content.

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Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data availability

A MS Excel file containing additional information on the taxa recorded from the literature and from entomological collections is available at: https://doi.org/10.48331/scielodata.NPDRGN

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Inventory

Selaginella P.Beauv. (Selaginellaceae) in the state of Maranhão, northeastern, Brazil: A floristic survey and a new record for the Cerrado domain

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Abstract: This work is a floristic study of *Selaginella* in Maranhão. The species survey is based on collections from fieldwork conducted between April 2006 and February 2023 and specimens from Maranhão deposited at the CCAA, HBRA, MG, and SLUI herbaria. Ten species were identified: *Selaginella conduplicata, S. convoluta, S. erythropus, S. flagellata, S. gynostachya S. marginata, S. minima, S. radiata, S. simplex,* and *S. sulcata.* We report the first record of *S. gynostachya* for Maranhão and the Cerrado domain in Brazil. Until now, this species was only known from areas of Amazonia. We provide a map with records, an identification key, and comments about the identification and geographic distribution of *Selaginella* species in Maranhão state. For the new record, we also provide photos.

Keywords: *floristics; gallery forest; lycophyte; Northeastern Brazil.*

Selaginella P.Beauv. (Selaginellaceae) no estado do Maranhão, nordeste, Brasil: Levantamento florístico e novo registro para o domínio Cerrado

Resumo: O presente trabalho trata do estudo florístico de *Selaginella* no Maranhão. O levantamento de espécies foi realizado com base em coletas de campo realizadas entre abril de 2006 e fevereiro de 2023 e em análise de espécimes coletados no Maranhão e depositadas nos herbários CCAA, HBRA, MG e SLUI. Foram identificadas 10 espécies: *Selaginella conduplicata, S. convoluta, S. erythropus, S. flagellata, S. gynostachya S. marginata, S. minima, S. radiata, S. simplex* e *S. sulcata.* Relatamos a primeira ocorrência de *S. gynostachya* para o Maranhão e também para o domínio do Cerrado Brasileiro. Até então essa espécie era registrada somente em áreas amazônicas. Neste artigo apresentamos um mapa com pontos de coleta, uma chave de identificação e comentários sobre a identificação, ecologia e distribuição geográfica para as espécies de *Selaginella* do Maranhão. Para o novo registro apresentamos também fotos.

Palavras-chave: *Florística; Licófitas; Mata de galeria; Nordeste do Brasil.*

Introduction

Selaginella P.Beauv. is the most speciose genus in the class Lycopodiopsida (lycophytes). It is estimated that there are approximately 700 species of *Selaginella*; the only genus in Selaginellaceae Wilk., which has a cosmopolitan distribution (PPGI 2016). However, the highest diversity of species is mostly found in the tropics (Jermy 1990, Valdespino 1993, Fraile et al. 1995).

In Brazil, *Selaginella* is represented by 97 species distributed in all phytogeographic domains, and with 38 species endemic to the country

(Góes-Neto et al. 2023). Most of the diversity of the genus in Brazil is in the Amazonia (53 spp.) and the Cerrado domains (11 spp.) (Góes-Neto et al. 2023). The Brazilian Cerrado is notoriously under-collected for all groups of plants, including those in protected areas. For Maranhão, recent studies have increased the number of known *Selaginella* from five (Góes-Neto et al. 2023) to nine species, most of which occur in the Cerrado (Almeida et al. 2020, Fernandes et al. 2022).

Studies about the genus in Brazil have mainly been concentrated on the Atlantic Forest and Amazonia (Bautista 1974a, b, Castellani & Freitas 1992, Hirai & Prado 2000, Prado & Freitas 2005, Prado & Hirai 2008, Heringer et al. 2016, Valdespino 2015a, b, Valdespino et al. 2015, Valdespino et al. 2018a, b, Valdespino 2020). Nevertheless, records from the Cerrado vegetation have been reported in the flora of the Distrito Federal (Hirai 2007), Minas Gerais (Heringer et al. 2016), and recent inventories in Maranhão (Almeida et al. 2020, Fernandes et al. 2022).

Selaginella is a taxonomically complex genus with many polymorphic species (Webster 1992). Additionally, there are some problems with the identification and classification of *Selaginella* species because they mainly are based on observations of herbarium specimens (Setyawan 2011). Alston et al. (1981) provided the last revision of *Selaginella* for tropical South America, including a key, synonymy, exsiccate, and taxa distribution. This work, however, does not include species descriptions, except for new taxa. Generally, the works used to identify neotropical *Selaginella* species are original descriptions and floras (Alston et al. 1981, Jermy 1990, Webster 1992, Valdespino 1992, Cremers & Boudrie 2007, Zhou & Zhang 2015, Heringer et al. 2016, Valdespino 2015a, b, Valdespino et al. 2015, Valdespino et al. 2018a, b, Valdespino 2020, Valdespino et al. 2022a, b, Góes-Neto et al. 2023). The infrageneric circumscription proposed by Jermy (1986, 1990) is widely accepted. In this, the author recognizes five subgenera: *Selaginella* P.Beauv*.*, *Ericetorum* Jermy*,* and *Tetragonostachys* Jermy, comprising isophyllous species, and *Stachygynandrum* (P.Beauv.) Baker, and *Heterostachys* Baker including anisophyllous species*. Selaginella* P.Beauv., *Ericetorum* Jermy, *Tetragonostachys* Jermy, *Stachygynandrum* (P.Beauv.) Baker, and *Heterostachys* Baker. Of these, the species in the first three are isophyllous and those in the last two are anisophyllous. Nevertheless, recent classifications proposed by Zhou & Zhang (2015) and Weststrand & Korall (2016) based on molecular phylogenetic studies suggest that some of the subgenera recognized by Jermy (1986, 1990) are not monophyletic. Nonetheless, these classifications differ in the number and circumscription of proposed subgenera. Zhou & Zhang (2015) classified the genus *Selaginella* into six subgenera (i.e., *Selaginella*, *Boreoselaginella*, *Pulviniella*, *Ericetorum*, *Heterostachys*, and *Stachygynandrum*), while Weststrand & Korall (2016) recognized seven (i.e., *Selaginella*, *Rupestrae*, *Lepidophyllae*, *Gymnogynum*, *Exaltatae*, *Ericetorum*, and *Stachygynandrum*). As a result, no agreement as to the infrageneric circumscription of the *Selaginella* exists and still there is a need for a comprehensive taxonomic revision of the genus, including an improved delimitation of species complexes.

The main taxonomic characters used to distinguish *Selaginella* from other lycophytes include the presence of rhizophores, microphylls with ligules at the base, heterospory, and reniform sporangia located adaxially (Jermy 1986, 1990, Webster 1992). In addition, *Selaginella* is ecologically well-adapted to inhabit various environments, such as humid tropical forests, deserts, and temperate forests. Furthermore, species of the genus can be terrestrial, rupicolous, and occasionally also epiphytic (Jermy 1990, Zhou & Zhang 2015, Heringer et al. 2016, Weststrand & Korall 2016).

The objective of this work is to provide a list of the *Selaginella* species occurring in the state of Maranhão, and to newly document the occurrence of a species previously undocumented for the Cerrado domain in Brazil for which a corresponding illustration. Furthermore, a key to identify currently known *Selaginella* species as occurring in the state of Maranhão is provided, as well as a distribution map for each of these taxa. Furthermore, under each species we provide comments related to habitat and distribution, as well as morphological characters to help identify them.

Material and Methods

Maranhão has a tropical, rainy climate (Alvares et al. 2013), average annual temperature between 25 and 26° C, average annual precipitation between 1400 and 1800 mm and is one of the states in northeastern Brazil with the lowest hydric deficit (Martins & Oliveira 2011). The dry period lasts five or six months (July to November or December), when the hydric deficit is 150–300 mm, and the rainy period also lasts five or six months (January to May or June) and is most intense between February and March (IMESC 2021).

Maranhão is an extremely relevant State in terms of biodiversity, housing three different phytogeographic domains, as well as transition areas between them, such as: Amazonia, occupying around 35% of the area of the state territory; Cerrado, around 64%; and Caatinga, around 1%. Furthermore, Maranhão has a large coastal region (around 640 km), also comprising floral elements characteristic of coastal zones, as well as transition zones towards the interior, between this large coastal region, and its continental phytogeographic domains, making the State ecosystems even more interesting and complex (Ab'Saber 2002, Rebêlo et al. 2003, Almeida & Vieira 2010, Spinelli-Araujo et al. 2016, Koerber et al. 2022, Vieira et al. 2023). Areas with *cocais* vegetation in Maranhão (where *Attalea speciosa* Mart. ex Spreng., the *babaçu* palm, is predominant) are locations modified by humans (Oren 1988, Santos-Filho et al. 2013).

The Amazonian region of Maranhão is part of the Belém Center of Endemism, with an area of 243,000 km^2, limited the Tocantins River to the west and the Pindaré River to the east. Less than a third of the forests in the Belém Center of Endemism are preserved, making it the most threatened area of endemism in Brazilian Amazon (Silva et al. 2005, Almeida & Viera 2010). The Cerrado in Maranhão is one of the most threatened areas in Brazil due to increased agricultural practices in the last decades, especially the cultivation of soybeans, corn and cotton (EMBRAPA, 2023). According to Castro & Martins (1999), Maranhão has the largest area of Cerrado in the Northeastern Brazil (328,366 km^2), corresponding to around 60% of the Cerrado in this region. Around 50% of the Brazilian Cerrado has been lost and what remains is becoming increasingly fragmented (Rodrigues et al. 2022).

This study is based on an analysis of material deposited in the CCAA, EAC, HBRA, MG, and SLUI herbaria (acronyms according to Thiers 2023) and field expeditions made between April 2006 and February 2023. The fieldwork was mainly conducted in the following protected areas and surroundings in Maranhão: Área de Proteção Ambiental Inhamum, Reserva Biológica do Gurupi, Parque Nacional Chapada das Mesas, Parque Estadual do Mirador, Reserva Extrativista

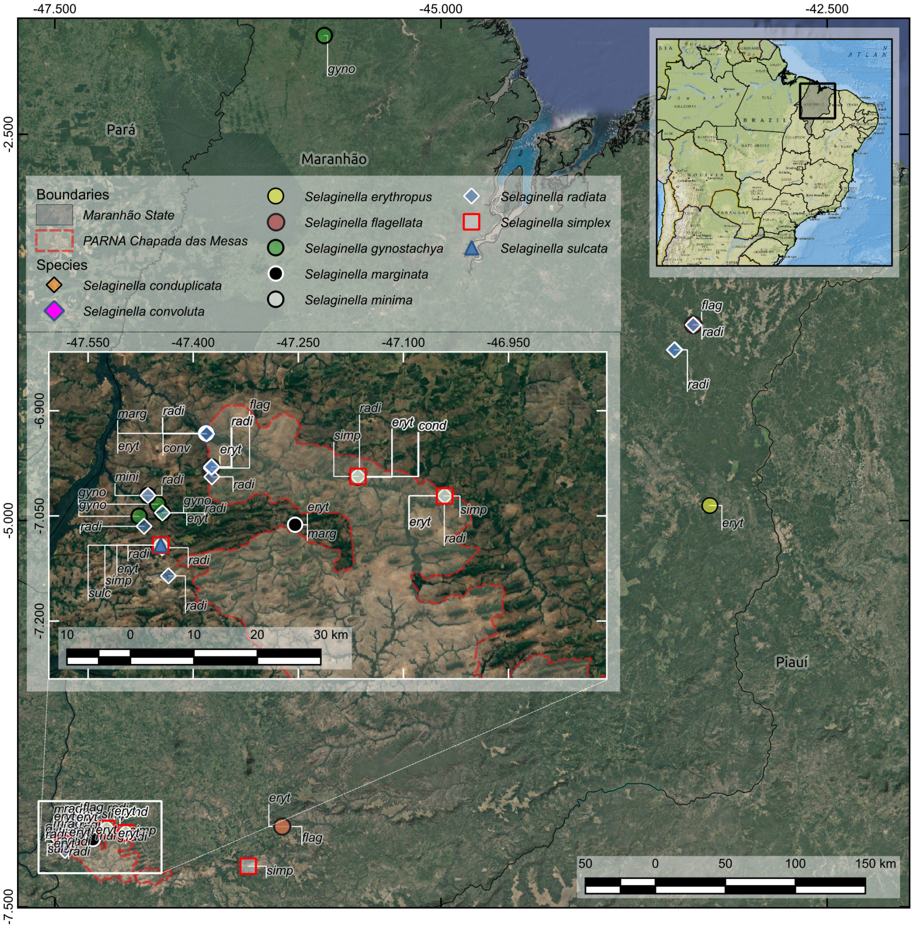

Figure 1. Map of the study area showing the sample sites of *Selaginella* in Maranhão and highlighting Chapada das Mesas National Park.

Chapada Limpa, and Área de Relevante Interesse Ecológico Itamacaoca (Figure 1).

The identification and distribution of the species were based on online databases and specialized literature, such as IPNI (2023), the Flora e Funga do Brasil 2023 monographs, and revisions and regional floras (e.g., Alston et al. 1981, Tryon & Stolze 1994, Moran & Riba 1995, Mickel et al. 2004, Hirai & Prado 2000, Cremers & Boudrie 2007, and Heringer et al. 2016). The terminology follows Lellinger (2002). The family delimitations are based on PPG I (2016). The nomenclature and authors of the species follow the International Plant Names Index (IPNI 2023).

Results

Ten species of *Selaginella* were identified to occur in Maranhão: *Selaginella conduplicata* Spring, *S. convoluta* (Arn.) Spring, *S. erythropus* (Mart.) Spring, *S. flagellata* Spring, *S. gynostachya* Valdespino, *S. marginata* (Humb. & Bonpl. ex Willd.) Spring, *S. minima* Spring, *S. radiata* (Aubl.) Spring, *S. simplex* Baker, and *S. sulcata* (Desv. ex Poir.) Spring ex Mart. Of these, *S. gynostachya* is a new record for Maranhão and the Brazilian Cerrado (Flora e Funga do Brasil 2023). The key below to identify species in Maranhão is based on material here studied and documented, followed by corresponding taxon information.

Identification key to the *Selaginella* species in Maranhão

1. Stem articulate; rhizophores dorsal; dorsal microphylls always auriculate, with one or two auricles..2

1’. Stem not articulate; rhizophores ventral, axillary, lateral, or rarely dorsal; dorsal microphylls not auriculate or rarely auriculate..4

2. Dorsal microphylls basifixed .... ***S. conduplicata***

2’. Dorsal microphylls peltate...3

3. Axillary microphylls peltate, base with a long auricle that is usually fimbriate or ciliate; lateral microphylls peltate, with a long auricle on the acroscopic portion .... ***S. marginata***

3’. Axillary microphylls basifixed, base with two denticulate to short-ciliate auricles; lateral microphylls basifixed, with two auricles, the acroscopic auricle more developed, the basiscopic auricle short .... ***S. sulcata***

4. Stem erect, forming a rosette.............…….............…. ***S. convoluta***

4’. Stem prostrate, ascendent, decumbent, suberect or erect, not forming a rosette...5

5. Stem of adult individuals red, reddish or pink, at least at the base until immediately above the first branch..............................***S. erythropus***

5’. Stem of adult individuals green, stramineous, or brown................6

6. Abaxial and adaxial microphyll surfaces conspicuously bicolor; axillary microphylls lanceolate; dorsal microphylls long-aristate ....***S. radiata***

6'. Abaxial and adaxial microphyll surfaces conspicuously concolorous; axillary microphylls ovate-lanceolate to oblong, oblong-ovate to ovate-elliptic or ovate to widely ovate; dorsal microphylls acute, short- to long-acuminate...7

7. Stem prostrate; lateral microphylls with a truncate base; axillary microphylls with a cordate base................................***S. gynostachya***

7'. Stem erect, ascendent to suberect; lateral microphylls with a rounded to subcordate base; axillary microphylls with a rounded base 8

8. Stem with flagelliform apex; dorsal microphylls with a long-aristate apex.. ***S. flagellata***

8'. Stem without a flagelliform apex; dorsal microphylls with an acute, acuminate, or long-acuminate apex..9

9. Lateral microphylls long-ciliate in the 1/2(–1/3) basal portion; axillary microphylls ciliate in the 1/3 basal portion, serrate to serrulate towards the apex…...***S. minima***

9'. Lateral microphylls denticulate in the lower 1/3, serrulate in the upper 2/3; axillary microphylls sparsely serrulate ……..……....….... ***S. simplex***

Selaginella conduplicata Spring

Specimens examined: BRAZIL, MARANHÃO, **Carolina**, PARNA Chapada das Mesas, Cachoeira do Prata, rio Farinha (bacia do rio Tocantins), ca. 6°59'37"S, 47°09'57"W, 197 m, 06 June 2018, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 03 (CCAA); idem. ca. 6°59'36,9"S, 47°9'58,5"W, 198 m, 12 March 2017, Silva, L.R. & Pietrobom, M.R. 43 (CCAA); idem. Silva, L.R. & Pietrobom, M.R. 40 (CCAA); idem. ca. 6°59'37,4"S, 47°09'58,0"W, 194 m, 29 October 2017, Silva, L.R. & Almeida, F.C. 84 (CCAA); idem. Estreito, PARNA Chapada das Mesas, Cachoeira do Prata, margem direita do rio Farinha, ca. 6°59'36,7"S, 47°9'53,1"W, 210 m, 06 June 2018, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 29 (CCAA/HBRA).

Identification. *Selaginella conduplicata* is characterized by the biauriculate lateral microphylls with a denticulate margin, generally more developed acroscopic auricle that overlap the stem and curves downward, and short, less evident, denticulate, basiscopic auricle, as well as the axillary microphylls with a biauriculate base and two, long, denticulate auricles that are generally unequal in size.

Habitat and distribution. Colombia, Venezuela, Guyana, Suriname, French Guiana, Peru, and Brazil (Acre, Amapá, Amazonas, Maranhão, Mato Grosso, Pará, Pernambuco, and Roraima). In the study area, it grows in gallery forests with rocky outcrops.

Selaginella convoluta (Arn.) Spring

Specimens examined: BRAZIL, MARANHÃO, **Carolina**, PARNA Chapada das Mesas, Cachoeira do Porão, ca. 06°55'55,6"S, 047°22'53,6"W, 174 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 31 (CCAA/HBRA). **Grajaú**, estrada para a cachoeira do Viriato, córrego com leito rochoso, 05°50'32"S, 46°07'36"W, 10 February 2023, A.W.C. Ferreira 1047 & D. O. Costa (SLUI).

Identification. *Selaginella convoluta* is mainly characterized by the rosette stem and very curled dry branches. Additionally, the lateral microphylls have a whitish acroscopic margin, which is generally fimbriate or ciliate throughout, and an acute, acuminate, or apiculate apex; microphylls have obscure idioblasts in the upper surfaces and, no stomata, and an acute to acuminate apex.

Habitat and distribution. Mexico, Guatemala, Honduras, Nicaragua, Cuba, Haiti, Dominican Republic, Colombia, Venezuela, Guyana, French Guiana, Peru, Brazil (Alagoas, Bahia, Ceará, Espírito Santo, Goiás, Mato Grosso do Sul, Maranhão, Minas Gerais, Paraíba, Paraná, Pernambuco, Piauí, Rio Grande do Norte, Rio de Janeiro, São Paulo, and Sergipe), Bolivia, Paraguay and Argentina. In the study area, this species grows in open gallery forests, on rocks, mainly in xeric environments exposed to the sun.

Selaginella erythropus (Mart.) Spring

Specimens examined: BRAZIL, MARANHÃO, **Carolina**, Resort da Pedra Caída, Cachoeira do Santuário Ecológico, ca. 07°02'44,2"S, 047°26'38,0"W, 128 m, 07 February 2020, Oliveira, S.S. & Pietrobom, M.R. 160 (CCAA); idem. Oliveira, S.S. & Pietrobom, M.R. 164 (CCAA/HBRA); idem. Oliveira, S.S. & Pietrobom, M.R 156 (CCAA/HBRA); idem. Topo do Morro do Dôdo, ca. 07°05'30,1"S, 047°26'46,8"W, 389 m, 06 February 2020, Oliveira, S.S. & Pietrobom, M.R. 130a (CCAA/HBRA); idem. PARNA Chapada das Mesas, Passagem da dona Lena, ca 07°03'45,1"S, 047°15'16,2"W, 230 m, 05 February 2020, Oliveira, S.S. & Pietrobom, M.R. 85 (CCAA); idem. Próximo a Cachoeira do Siduca, ca. 06°58'54,1"S, 047°22'26,8"W, 241 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 43 (CCAA); idem. Cachoeira do Porão, ca. 06°55'55,6"S, 047°22'53,6"W, 174 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 33 (CCAA); idem. Cachoeira do Prata, rio Farinha, ca. 6°59'37,4"S, 47°09'58,0"W, 194 m, 29 October 2017, Silva, L.R. & Almeida, F.C. 91 (CCAA); idem. Silva, L.R. & Almeida, F.C. 90 (CCAA); idem. Silva, L.R. & Almeida, F.C. 100 (CCAA); idem. ca. 6°59'36,9"S, 47°9'58,5"W, 198 m, 12 March 2017, Silva, L.R. & Pietrobom, M.R. 39 (CCAA); idem. ca. 6°59'37"S, 47°09'57"W, 197 m, 06 June 2018, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 08 (CCAA); idem. Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 14 (CCAA); idem. Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 09 (CCAA); idem. ca. 6°59'41,3"S, 47°9'57,4"W, 213 m, 12 March 2017, Silva, L.R. & Pietrobom, M.R. 37 (CCAA); idem. Cachoeira da Ponta da Serra, riacho Lajes, ca. 6°58'47,4"S, 47°22'25"W, 235 m, 11 October 2017, Silva, L.R. & Pietrobom, M.R. 24 (CCAA); idem. Silva, L.R. & Pietrobom, M.R. 29 (CCAA); idem. Cachoeira São Romão, rio Farinha, ca. 7°01'15,4"S, 47°02'28,2"W, 241 m, 31 October 2017, Silva, L.R. & Almeida, F.C. 183 (CCAA); idem. ca. 7°01'17,1"S, 47°02'27,1"W, 256 m, 07 June 2018, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 65 (CCAA); idem. Estreito, PARNA Chapada das Mesas, Cachoeira do Prata, margem direita do rio Farinha, ca. 6°59'36,7"S, 47°9'53,1"W, 210 m, 06 June 2018, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 26 (CCAA); idem. Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 28 (CCAA); idem. **Caxias**, Povoado Altos, 01 April 2006, R. S. Fernandes 73 (EAC, MG); Correntinho, 27 May 2007, R. S. Fernandes et al. 92 (MG, EAC); idem. **Fortaleza dos Nogueiras**, cachoeira Castanhão, ca. 06°58'51"S, 46°01'42"W, 20 February 2022, A.W.C. Ferreira, 522, 523 (CCAA).

Identification. *Selaginella erythropus* is characterized by the dark red to reddish stem, patent to ascendent lateral microphylls that are ovate in the most basal portion, and become ovate-lanceolate, lanceolate or slightly falcate towards the apex of the branch, acroscopic margin that is hyaline and ciliate along the basal portion and denticulate along the apical portion, and basiscopic margin that is greenish, narrowly hyaline, and entire or denticulate to serrulate along the apical portion.

Habitat and distribution. Costa Rica, Colombia, Ecuador, Peru, Brazil (Bahia, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Piauí, Rio Grande do Norte, Rio de Janeiro, and Tocantins) and Bolivia. In the study area, it grows in closed gallery forests in sandy soils and on rocks near waterfalls.

Selaginella flagellata Spring

Specimens examined: BRAZIL, MARANHÃO, **Carolina**, PARNA Chapada das Mesas, próximo a Cachoeira do Siduca, ca. 06°58'54,1"S, 047°22'26,8"W, 241 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 46 (CCAA); idem. Chapadinha, Localidade Xororó, 14 September 2022, M.A F. Rodrigues & A.L.F. Rodrigues, 41 (CCAA); Localidade Xororó, 10 September 2016, M.A.F. Rodrigues & A.L.F. Rodrigues, 16 (CCAA); idem. **Caxias**, Povoado Altos, 01 April 2006, R. S. Fernandes 72 (EAC, MG); **Fortaleza dos Nogueiras**, cachoeira Castanhão, ca. 06°58'51"S e 46°01'42"W, 20 February 2022, A.W.C. Ferreira, 520 (CCAA).

Identification. *Selaginella flagellata* is characterized by the long-aristate dorsal microphylls, with an arista that is often half the length of the microphyll and an asymmetric base that sometimes forms a short external auricle, and axillary microphylls with conspicuously hyaline margins that are ciliate at the base and turn denticulate towards the apex. Sterile individuals of the species can be identified by the stem apex which is usually flagelliform.

Habitat and distribution. Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Trinidad and Tobago, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil (Acre, Amapá, Amazonas, Maranhão, Mato Grosso, Pará, Piauí, Rondônia, and Tocantins) and Bolivia. In the study area, this species grows in closed gallery forests, in sandy ravines, and almost always in shady areas.

Selaginella gynostachya Valdespino

Figure S1

New records: BRAZIL – MARANHÃO, **Cândido Mendes**, Fazenda Sete Irmãos, 1°51'39.7"S, 45°45'21.5"W, 56 m alt.; 26 October 2019; W.R. Silva Junior, A.W.C. Ferreira 154 (SLUI); idem. 26 October 2019; W.R. Silva Junior, A.W.C. Ferreira 155; (CCAA); idem. 26 October 2019; W.R. Silva Junior, A.W.C. Ferreira 290; (CCAA); idem. **Carolina**, Resort da Pedra Caída, Cachoeira do Santuário Ecológico, ca. 07°02'44,2"S, 047°26'38,0"W, 128 m, 07 February 2020, Oliveira, S.S. & Pietrobom, M.R. 142 (CCAA/HBRA); idem. Oliveira, S.S. & Pietrobom, M.R. 144 (CCAA/HBRA); idem. Oliveira, S.S. & Pietrobom, M.R. 152 (CCAA/HBRA); idem. Oliveira, S.S. & Pietrobom, M.R. 159 (CCAA/HBRA); idem. Cachoeira da Pedra Furada, ca. 07°01'59,3"S, 047°27'01,9"W, 195 m, 07 February 2020, Oliveira, S.S. & Pietrobom, M.R. 175 (CCAA/HBRA); idem. Oliveira, S.S. & Pietrobom, M.R. 176 (CCAA/HBRA); idem. Cachoeira do Capelão, ca. 07°03'01,5"S, 047°28'37,9"W, 216 m, 07 February 2020, Oliveira, S.S. & Pietrobom, M.R. 199 (CCAA/HBRA); idem, cachoeira do Garrote, 07°01'01"S, 47°28'38"W, 11 March 2022, A.W.C. Ferreira 576.

Identification. The presence of idioblasts in the upper surface of the axillary microphylls and the denticulate to ciliate-denticulate margins of the lateral microphylls are variable characteristics that must be carefully observed (Cremers & Boudrie 2007).

Selaginella gynostachya, a species recently recorded for Brazil (Góes-Neto et al. 2015), resembles *S. karowtipuensis* Valdespino (which occurs in Guyana). However, the latter differs because it has dorsal microphylls with a subcordate to rounded base, idioblasts in the upper surface of the lateral microphylls and dorsal microphylls with a long-acuminate to short-aristate apex, while *S. gynostachya* has dorsal microphylls with a sub-truncate to rounded base, lacks idioblasts in the upper surface of the lateral microphylls, and has elliptic to ovate-elliptic or widely ovate dorsal microphylls with an acute to short-acuminate apex. This is the first record of this species for the Brazilian Cerrado and Maranhão. Previous records are all from areas in Amazonia, Brazil (Flora e Funga do Brasil 2023).

Habitat and distribution. Venezuela, Guyana, French Guiana, and Brazil. In Brazil, this species was known only from Amazonia, in Pará (Flora e Funga do Brasil 2023), and it is now also known to occur in the Cerrado in Maranhão. In the study area, *S. gynostachya* grows in closed gallery forests near water courses and on rocks near waterfalls.

Selaginella marginata (Humb. & Bonpl. ex Willd.) Spring

Specimens examined: BRAZIL, MARANHÃO, **Carolina**, PARNA Chapada das Mesas, Passagem da dona Lena, ca. 07°03'45,1"S, 047°15'16,2"W, 230 m, 05 February 2020, Oliveira, S.S. & Pietrobom, M.R. 89 (CCAA/HBRA); idem. Cachoeira do Porão, ca. 06°55'55,6"S, 047°22'53,6"W, 174 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 29 (CCAA/HBRA).

Identification. *Selaginella marginata*, in addition to its articulate stem, is characterized by the lateral microphylls with an auriculate base, with a long auricle on the acroscopic portion that is curved towards the base, and axillary microphylls with a long auricle on the base that is almost always fimbriate or ciliate.

Habitat and distribution. Mexico, Venezuela, Brazil (Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Piauí, Rio de Janeiro, Rio Grande do Sul, Rondônia, Santa Catarina, São Paulo, and Tocantins), Bolivia, Paraguay and Argentina, Uruguay. In the study area, it grows in the interior of gallery forests and on rocky outcrops exposed to light near waterfalls.

Selaginella minima Spring

Specimens examined: BRAZIL, MARANHÃO, **Carolina**, Estância Ecológica Vereda Bonita, ca. 07°01'14,8"S, 047°27'52,6"W, 191 m, 06 February 2020, Oliveira, S.S. & Pietrobom, M.R. 90 (CCAA/HBRA).

Identification. *Selaginella minima* is 1–9 cm tall and has totally dimorphic microphylls along the length of its stem. The margins of the lateral and dorsal microphylls and sporophylls have 2 to 5 rows of idioblasts that give the border of the leaves a whitish appearance. The dorsal microphylls are ovate and have an asymmetric (the internal base tends to be truncate and the external base forms a poorly differentiated external auricle) or oblique base, margins that are serrate to finely serrate or short-ciliate along the proximal half and finely serrate along the distal half, with an internal side that is serrate to finely serrate, and an apex that is acute to acuminate. In addition, rarely, there are scattered, short trichomes on the upper surface of the lateral microphylls, mainly towards the basiscopic half of the lamina (see the illustration of this species in Mickel et al. 2004, fig. 271).

Habitat and distribution. Mexico, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Trinidad and Tobago, French Guiana, Brazil (Amapá, Amazonas, Goiás, Maranhão, Mato Grosso, Pará, Piauí, and Rondônia) and Bolivia. In the study area, it grows in closed gallery forests on rocks (with almost no organic material) exposed to light.

Selaginella radiata (Aubl.) Spring

Specimens examined: BRAZIL, MARANHÃO, **Carolina**, Estância Ecológica Vereda Bonita, ca. 07°01'14,8"S, 047°27'52,6"W, 191 m, 06 February 2020, Oliveira, S.S. & Pietrobom, M.R. 100 (CCAA); idem. Resort da Pedra Caída, rio Vão Feio, próximo a Cachoeira da Caverna, ca. 07°03'53,2"S, 047°28'12,6"W, 200 m, 07 February 2020, Oliveira, S.S & Pietrobom, M.R. 187 (CCAA/HBRA); idem. Cachoeira do Santuário Ecológico, ca. 07°02'44,2"S, 047°26'38,0"W, 128 m, 07 February 2020, Oliveira, S.S. & Pietrobom, M.R. 161 (CCAA); idem. Cachoeira do Dôdo, ca. 07°05'43,0"S, 047°26'39,5"W, 234 m, 06 February 2020, Oliveira, S.S. & Pietrobom, M.R. 118 (CCAA/HBRA); idem. Topo do Morro do Dôdo, ca. 07°05'30,1"S, 047°26'46,8"W, 389 m, 06 February 2020, Oliveira, S.S. & Pietrobom, M.R. 130b (CCAA/HBRA); idem. Morro do Dôdo, ca. 07°05'39,3"S, 047°26'39,3"W, 256 m, 06 February 2020, Oliveira, S.S. & Pietrobom, M.R. 126 (CCAA/HBRA); idem. Oliveira, S.S. & Pietrobom, M.R. 121 (CCAA/HBRA); idem. Entorno do PARNA Chapada das Mesas, riacho da RPPN Mansinha, ca. 7°08'07,7"S, 47°26'07,1"W, 286 m, 08 June 2018, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 126 (CCAA); idem. Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 120 (CCAA/HBRA); idem. PARNA Chapada das Mesas, Cachoeira do Porão, ca. 06°55'55,6"S, 047°22'53,6"W, 174 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 24 (CCAA/HBRA); idem. próximo a Cachoeira do Porão, ca. 06°55'58,2"S, 047°22'50,8"W, 175 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 36 (CCAA/HBRA); idem. ca. 06°55'58,2"S, 047°22'50,8"W, 175 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 39 (CCAA); idem. próximo a Cachoeira do Siduca, ca. 06°58'54,1"S, 047°22'26,8"W, 241 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 50 (CCAA/HBRA); idem. Riacho Lajes, próximo a Cachoeira do Siduca, ca. 06°59'38,99"S, 047°22'23,9"W, 243 m, 04 February 2020, Oliveira, S.S. & Pietrobom, M.R. 58 (CCAA/HBRA); idem. Cachoeira São Romão, ca. 7°1'17,2"S, 47°2'27,8"W, 258 m, 13 March 2017, Silva, L.R. & Pietrobom, M.R. 59 (CCAA/MG); idem. Silva, L.R. & Pietrobom, M.R. 55 (CCAA/MG); idem. 7°01'17,1"S, 47°02'27,1"W, 256 m, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 47 (CCAA); idem. Cachoeira da Ponta da Serra, riacho Lajes, ca. 6°58'47,4"S, 47°22'25"W, 235 m, 11 March 2017, Silva, L.R. & Pietrobom, M.R. 22 (CCAA/MG); idem. ca. 6°58'47,1"S, 47°22'25,5"W, 238 m, 08 June 2018, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 114 (CCAA); idem. **Estreito**, PARNA Chapada das Mesas, margem direita do rio Farinha, ca. 6°59'36,7"S, 47°9'53,1"W, 210 m, 12 March 2017, Silva, L.R. & Pietrobom, M.R. 47 (CCAA/MG); idem. **Chapadinha**, próximo ao Povoado Cumprido, 22 February 2022, R.S. Fernandes & NA Mendonça 17 (CCAA); Estrada Próximo ao Riacho da Raiz, 22 February 2022, R.S. Ottoni & NA Mendonça 14 (CCAA); Povoado Centro Velho, 29 March 2022, J.A.S. SILVA 396a (CCAA); RESEX Chapada Limpa, Povoado Mata do Jeroca, 17 July 2019, JAS Silva 392a (CCAA); RESEX Chapada Limpa, Povoado Mata do Jeroca, 11 July 2019, R.S. Fernandes 1070 (CCAA); Povoado Centro Velho, 29 March 2022, J.A.S. Silva 396 (CCAA); Estrada próximo ao Riacho da Raiz, 23 August 2022, N.A. Mendonça & RS Fernandes 33 (CCAA).

Identification. *Selaginella radiata* is characterized by dorsal microphylls that are widely elliptic to widely orbicular with a rounded to subcordate base, arched central vein, making the inner half of the lamina wider than the outer half of the lamina, long, grooved apex (1/4–3/4 of the lamina length), and upper surface with more visible stomata (easily seen in specimens not preserved in alcohol). Additionally, the upper surface of the dorsal and lateral microphylls often have idioblasts that are difficult to see in specimens preserved in alcohol. The margins of the dorsal microphylls are long-ciliate, at least along the proximal 1/3–1/2 (to 3/4) of the lamina. Further, it has an erect habit and is at least 30 cm tall, the sporophyte is deltoid and 3–4-pinnate, and the microphylls on the main stem, until the first branch, tend to look monomorphic.

Habitat and distribution. Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador and Brazil (Amapá, Amazonas, Bahia, Maranhão, Mato Grosso, Pará, Piauí, and Rondônia). In the study area, it grows in wet soils and the shade in gallery forests and on rocky outcrops.

Selaginella simplex Baker

Specimens examined: BRAZIL, MARANHÃO, **Estreito**, PARNA Chapada das Mesas, Cachoeira do Prata, margem direita do rio Farinha, ca. 6°59'36,7"S, 47°9'53,1"W, 210 m, 06 June 2018, Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 25 (CCAA); idem. Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 30 (CCAA); idem. Almeida, F.C.; Silva, J.A.S.; Oliveira, L. & Ottoni, F. 27 (CCAA/HBRA); idem. 12 March 2017, Silva, L.R. & Pietrobom, M.R. 48 (CCAA/MG); idem. Silva, L.R. & Pietrobom, M.R. 46 (CCAA/MG); idem. Cachoeira São Romão, ca. 7°1'17,2"S, 47°2'27,8"W, 258 m, 13 March 2017, Silva, L.R. & Pietrobom, M.R. 58 (CCAA/MG); idem. **Carolina**, Topo do Morro do Dôdo, ca. 07°05'30,1"S, 047°26'46,8"W, 389 m, 06 February 2020, Oliveira, S.S. & Pietrobom, M.R. 129 (CCAA/HBRA); idem. **Nova Colinas**, Parque Aquático Três Marias, ca. 07°14'14"S e 46°14'55"W, 22 February 2022, A.W.C. Ferreira 520 (CCAA).

Identification. *Selaginella simplex* is a small, delicate plant that reaches 5 cm long. It can also be characterized by the ovate to ovate-elliptic lateral microphylls with a rounded base, acroscopic base sometimes overlapping the stem, acroscopic margin greenish, narrowly hyaline, denticulate at the base, serrulate towards the apex, basiscopic margin greenish, narrowly hyaline, serrulate mainly along the upper middle, and lower surface of the lateral microphylls occasionally with idioblasts. The dorsal microphylls are around 1.0 mm apart and have margins that are greenish, narrowly hyaline and denticulate, an upper surface without idioblasts or stomata, and an acuminate to long-acuminate apex.

Habitat and distribution. Mexico, Costa Rica, Panama, Venezuela, Trinidad and Tobago, Ecuador, Brazil (Bahia, Goiás, Maranhão, Mato Grosso, Pará, Pernambuco, and Sergipe) and Bolivia. It occurs in gallery forests in sandy, wet ravines and on wet rocks near waterfalls.

Selaginella sulcata (Desv. ex Poir.) Spring ex Mart.

Material Examined. BRAZIL, MARANHÃO, **Carolina**, Topo do Morro do Dôdo, ca. 07°05'30,1"S, 047°26'46,8"W, 389 m, 06 February 2020, Oliveira, S.S. & Pietrobom, M.R. 130 (CCAA/HBRA).

Identification. *Selaginella sulcata* is characterized by lateral microphylls with a biauriculate base, acroscopic auricle generally more developed, overlapping the stem, curved towards the bottom, denticulate to short-ciliate, basiscopic auricle short, less evident, denticulate to short-ciliate, base of dorsal microphylls auriculate, with one or two auricles, external auricle more developed, auricles denticulate to short-ciliate, and base of the axillary microphylls with two denticulate to short-ciliate auricles.

Habitat and distribution. Suriname, French Guiana, Peru, Brazil (Acre, Alagoas, Amapá, Amazonas, Bahia, Ceará, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo), Bolivia, Paraguay and Argentina. In the study area, it grows in closed gallery forest, on rock walls, almost always in the shade.

Discussion

The representatives of *Selaginella* in Maranhão mainly occur in the Cerrado region where there are nine recorded species (Fernandes et al. 2022); there is only one recorded species in the Amazonian region (Silva Junior et al. 2020, Goés-Neto et al. 2023). The first record of *S. gynostachya* for the Cerrado domain in Brazil shows that this region is under-collected, as noted by Fernandes et al. (2022) in a floristic study of ferns and lycophytes in the region of Chapada das Mesas. The occurrence of *S. gynostachya* in the ecotonal zone in Maranhão also demonstrates that individuals of this species can adapt and colonize a greater diversity of microenvironments and microclimates. This species has also been observed in an area of Amazonia in Maranhão. In this domain, *S. gynostachya* was collected as a terrestrial plant on the margin of a seasonal stream, while in the Cerrado in Maranhão it was mainly found as a rupicolous plant near waterfalls. The common factor in these areas was the presence of humidity and shade provided by the canopy.

Before this study, the only survey specifically about lycophytes in Maranhão was conducted in the region of Chapada das Mesas (Almeida et al. 2020), which recorded six species, including four Sellaginelaceae: *Selaginella conduplicata* Spring, *S. erythropus* (Mart.) Spring, *S. radiata* (Aubl.) Baker, and *S. simplex* Baker. Almeida et al. (2020) also recorded *S. conduplicata* and *S. radiata* for the first time for the Cerrado phytogeographic domain in Brazil, and *S. conduplicata* was a new record for Maranhão. Another study about ferns and lycophytes in Maranhão, which was also conducted in the region of Chapada das Mesas (Fernandes et al. 2022), recorded 17 species of lycophytes, including 12 species of *Selaginella* (three not identified). Of these, three were new records for Maranhão: *Selaginella convoluta* (Arn.) Spring, *S. minima* Spring., and *S. sulcata* (Desv. ex Poir.) Spring ex Mart.

For the present study, which was based on previous surveys and new collections, we recorded ten *Selaginella* species, of which *S. gynostachya* is a new record for Maranhão and the Brazilian Cerrado. Despite this new record, for plants, there are still many poorly sampled areas in Maranhão and we expect that this number of *Selaginella* species and the numbers for other plant species will increase.

Various recent floristic studies confirm that Maranhão is under-collected (Ferreira et al. 2017, Ferreira et al. 2018, Ferreira et al. 2019a, b, Ferreira et al. 2022, Gomes et al. 2021, Guarçoni et al. 2018a, b, Guarçoni et al. 2020, Oliveira et al. 2021, Oliveira et al. 2022, Pessoa et al. 2022, Scatigna et al. 2020, Silva et al. 2022). There are few surveys of the fern and lycophyte species in Maranhão (Almeida et al. 2020, Silva Junior et al. 2020, Fernandes et al. 2022), suggesting the need for new botanical studies in the state to update the Flora e Funga do Brasil database, which currently only lists five *Selaginella* species.

Supplementary Material

The following online material is available for this article:

Figure S1 – *Selaginella gynostachya* Valdespino. A. Habit. B. Part of the stem showing an axillary rhizophore. C. Axillary microphyll. D. Dorsal microphyll. E. Lateral microphyll. F. Dorsal sporophylls with microspores (L.R. Silva & M.R. Pietrobom 39 [CCAA819]). Scale bar: A = 1cm; B = 0.5 mm; C; D; E; F = 1 mm.

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Conflicts of Interest

We have no conflict of interest.

Data Availability

Supporting data are available at <https://data.scielo.org/dataset.xhtml?persistentId=doi:10.48331/scielodata.PKGQSM>.

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Short Communication

Georeferenced database and interactive online map of limnoterrestrial and freshwater Tardigrada from Central and South America

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Abstract: Like other meiofaunal organisms, tardigrades suffer from a significant knowledge gap concerning many aspects of their biodiversity. The lack of an up-to-date digital collection with all species and details of limnoterrestrial and freshwater tardigrades in South and Central America is one of the most critical gaps to be filled. Therefore, the present work aims to develop a database containing all valid species of limnoterrestrial and freshwater tardigrades from South and Central America found until 2023 and provide open access to the results. Data for each species were obtained directly from the literature using Google Scholar and the website tardigrada.net. This compiled data resulted in the creation of a database with the species name, author and year of species description, genus, family, class, type country, type location, coordinates (longitude and latitude), if it is aquatic and/or limnoterrestrial, substrate where it was found, the country and location of collection, and manuscript containing the species identification. Furthermore, the coordinates of each occurrence were plotted on maps with political-administrative boundaries and Neotropical and Andean biogeographic regions. In addition, statistical analysis was performed related to the geographic distribution of the sampling effort. From the literature, 2157 records of valid non-marine Tardigrada species, endemic or not, were computed. From these records, 271 species of tardigrades have been identified in the two regions combined, with 223 species in South America and 129 species in Central America. We were able to show that there are still many biases in the sampling of tardigrades in the Neotropical and Andean regions and that further studies are needed on the biogeography of these meiofaunal organisms in these biogeographic regions. We expect this database to help better understand the richness and distribution patterns of limnoterrestrial and aquatic tardigrade species in Central and South America.

Keywords: *meiofauna; tardigrades; biogeography; Neotropical; sampling effort.*

Banco de dados georreferenciado e mapa interativo online de Tardigrada terrestres e aquáticos da América Central e América do Sul

Resumo: Tardígrados, assim como outros organismos meiofaunais, possuem uma lacuna de conhecimento significativa acerca de muitos aspectos da sua biodiversidade. A inexistência de um acervo digital, e atualizado, com todas as espécies e detalhes de tardígrados limnoterrestres e aquáticos na América Central e Sul é uma das lacunas mais importantes a serem preenchidas. Dessa maneira, o presente trabalho tem como objetivo elaborar e disponibilizar, de maneira gratuita, um banco de dados contendo todas as espécies válidas de tardígrados limnoterrestres e aquáticos das América do Sul e América Central encontradas até 2023. Os dados de cada espécie foram obtidos diretamente na literatura, utilizando o Google Scholar e o site tardigrada.net. Com todos esses dados compilados, foi elaborado um banco de dados com nome da espécie, autor e ano de descrição da espécie, gênero, família, classe, país tipo, local tipo, coordenadas (longitude e latitude), se é aquático e/ou limnoterrestre, substrato onde foi encontrado, país coletado, local de coleta e manuscrito com a identificação da espécie. Ademais, as coordenadas obtidas de cada ocorrência foram plotadas em mapas das fronteiras político-administrativas e das regiões biogeográficas Neotropical e Andina. Além disso, uma análise estatística quanto à distribuição geográfica do esforço amostral foi feita. Da literatura, foram computados 2157 registros de espécies válidas de tardígrados limnoterrestre, endêmicas ou não. Desses registros, foram descobertas, até hoje, 271 espécies de tardígrados entre as duas regiões, com 223 espécies na América do Sul e 129 espécies na América Central. Foi possível demonstrar que ainda há muito viés na amostragem de tardígrados nas regiões Neotropical e Andina, e mais estudos acerca da biogeografia desses organismos meiofaunais nessas regiões biogeográficas são necessários. A partir desse banco de dados, espera-se contribuir para um maior entendimento da riqueza e dos padrões de distribuição de espécies de tardígrados limnoterrestres e aquáticos nas América Central e Sul.

Palavras-chave: *meiofauna; tardígrados; biogeografia; Neotropical; esforço amostral.*

Introduction

Water bears are free-living, microscopic animals (about 50-1200 µm in size) that belong to the phylum Tardigrada and are divided into the classes Heterotardigrada and Eutardigrada (Nelson et al. 2020). They have segmented bodies with four pairs of legs and inhabit terrestrial, aquatic, and marine environments (Peluffo et al. 2007, Vicente & Bertolani 2013, Schill 2018, Bartels et al. 2020, Nelson et al. 2020). Most tardigrade species are limnoterrestrial, inhabiting mosses, lichens, leaf litter, and soil; however, some are aquatic, living in sediments or roots of aquatic plants in inland waters or marine sediments from the intertidal zone to abyssal depths (Guil & Cabrero-Sañudo 2007, Schill 2018, Bartels et al., 2020, Nelson et al. 2020).

Like other meiofaunal organisms, tardigrades suffer from the "meiofauna paradox". They are animals believed to have a cosmopolitan distribution but without dispersal capabilities (Giere, 2008). At the same time, the "Everything is everywhere, but environment selects" (EiE) hypothesis (Finlay et al. 1996, Fenchel et al. 1997, Fenchel & Finlay 2004) was widely accepted for small metazoans, implying the absence of any discernible biogeographic pattern (Cerca et al. 2018, Morek et al. 2021). Most available data on tardigrade species distribution has barely any records which were identified utilizing an integrative taxonomic approach; this hinders the delimitation of species and the understanding of their distribution patterns (Morek et al. 2019, Gąsiorek et al. 2019a). Thus, it is essential to utilize both molecular and observational data to better comprehend tardigrade species distribution patterns (Gąsiorek et al. 2019a).

The presence of a geographic sampling bias and the fact that only a few species have been studied make it difficult to understand the limits of dispersal and, consequently, the distribution patterns and richness of tardigrades, especially in the Southern Hemisphere (Bini et al. 2006, Guil et al. 2009, Yang et al. 2013, Cerca et al. 2018, Azovsky et al. 2020, Garraffoni et al. 2021). In the Neotropical region, the number of recorded limnoterrestrial tardigrade species is much lower compared to other regions, mainly due to the scarce number of specialized researchers, which in turn reduces the number of studies conducted there (Guil & Cabrero Sañudo 2007, Fontaneto et al. 2012, Nelson et al. 2020, Garraffoni et al. 2021).

Kaczmarek et al. (2014, 2015) compiled the records of non-marine tardigrades in Central and South America up to the respective years of their publication. However, updating the data, and facilitating access and use is necessary. Therefore, this study presents a georeferenced database created through an extensive literature search of all limnoterrestrial and freshwater tardigrades in Central and South America, along with statistical analyses and maps to represent their distribution graphically. This digital and updated collection of the occurrence data of limnoterrestrial and freshwater tardigrades in Central and South America will undoubtedly benefit future biology studies or large-scale analyses and interpretations of biodiversity and distribution data of tardigrades in the Neotropics.

Material and Methods

Distribution data for limnoterrestrial and freshwater tardigrades was mainly obtained from Kaczmarek et al. (2014), who listed all non-marine tardigrades from Central America, and Kaczmarek et al. (2015) from South America. In addition, a literature search was conducted from 2014 to 2023 using Google Scholar and the "Recent papers" section of tardigrada.net. A set of terms was used to try to locate all possible publications that had limnoterrestrial tardigrade species as the central topic: "south american limnoterrestrial tardigrade OR central american limnoterrestrial tardigrade OR new south american tardigrade species OR new central american tardigrade species OR limnoterrestrial tardigrade south america OR limnoterrestrial tardigrade central america OR new species limnoterrestrial tardigrade south america OR new species limnoterrestrial tardigrade central america".

For our final dataset, we removed all records from species that present any kind of taxonomical problem (e.g. unknown type material, dubious name, dubious species and/or descriptions with insufficient morphological data) cited in Kaczmarek et al. (2014, 2015) or in the most updated checklist of Tardigrada species organized by Degma & Guidetti (2023) (Table S2). Species records that contained names with c.f. were also not used. Furthermore, we grouped the species sampled in both regions into endemic (i.e. *locus typicus* is in Central or South Americas) and traditionally treated as allegedly cosmopolitan (i.e. *locus typicus* is outside of Central and South America; usually records of those species are scattered across the globe and unreliable in the light of modern tardigrade systematics) since many recent studies showed that records of species are prone to contain misidentifications (e.g. Michalczyk et al. 2012, Morek et al. 2019, Morek et al. 2021).

To visualize the reported locations of all species, we plotted geographic coordinates on two maps, one shows reported localities from both sections, and the other contains the number of records in each area. Maps were elaborated for both geopolitical boundaries and biogeographic regions in Central and South America. For the latter maps, we used the Andean and Neotropical provinces proposed by Morrone (2015a) and Morrone et al. (2022), respectively. The data on the biogeographic regions map had to be adjusted (removal of 27 records and four species) because northern Mexico is not fully represented in the Neotropical region. In addition, an interactive and free-to-use online map was created, where each point represents a sampling site of a single species. For this map, sampling sites were flagged in three ways: putatively cosmopolitan, endemic or taxonomic problems. Additionally, we created charts of observed species richness from published articles for countries and biogeographic provinces to illustrate the relationship between observed species richness and sampling effort.

We merged shapefiles from the Andean and Neotropical biogeographic regions produced by Löwenberg-Neto (2015) and Morrone et al. (2022). This procedure yields duplicate provinces that overlap (transition zone). The Neotropical South American transition zone (Atacama, Comechigones, Cuyan High Andean, Desert, Monte, Paramo and Puna provinces) was kept to solve this, while the same Andean unit was removed (Atacama, Desert, Monte, Paramo, Prepuna, and Puna provinces).

For the elaboration of the maps and charts in this article, we used R v4.3.0 (R Core Team 2023), Rstudio v2023.3.1.446 (Posit Team 2023), and the packages ggpubr v0.6.0 (Kassambara 2023), tmap v3.3-3 (Tennekes 2018), sf v1.0-13 (Pebesma 2018), rnaturalearth v0.3.2.9000 (South 2017), rnaturalearthdata v0.2.1 (South 2022), and tidyverse v1.3.0 (Wickham et al. 2019). We also used ArcGIS online (2023) for the interactive map.

Results

Between 2014 to 2023, we found nine published papers regarding descriptions of new species and new records in Central America, while in South America, there were 27 (Table S1).

With all this data compiled, the database is a comma-separated value (.csv) file consisting of a single table with 19 columns:

- Species: taxon of the collected species;
- Author and year of species' description: name(s) of the author(s) and year of species description;
- Genus: taxon of the species' genus;
- Family: taxon of the species' family;
- Class: taxon of the species' class;
- Type country: country of the collected specimen that gave the species its name;
- Type location: geographic location of the collected specimen that gave the species its name;
- Longitude (Lon): longitude of the species' occurrence;
- Latitude (Lat): latitude of the species' occurrence;
- Aquatic or limnoterrestrial: defines whether the species is limnoterrestrial or aquatic;
- Substrate where it was found: divided into six columns, there are three primary substrates (moss, lichen, and others) with a column for each, followed by another column describing the location of the collected substrate;
- Country of collection: the country where the occurrence of the species was documented;
- Place of collection: geographic location where the occurrence of the species was documented;
- Manuscript containing the species' identification: work in the literature that recorded the occurrence of the species.

Valid species records of non-marine Tardigrada from South and Central America, endemic or not, totalized 271 species, of which 129 were found in Central America (33 endemic) and 223 in South America (110 endemic), amounting to 2157 sampling sites (Figure 1A). A total of 141 endemic species corresponded with 732 sites (Figure 1C), while 130 were "cosmopolitan" ones that were recorded at 1425 sites (Figure 1E). The occurrence of substantial sampling effort for endemic species was noticed in Costa Rica (212 records), Argentina (176 records), and Colombia (77 records) (Figure 1D). "Cosmopolitan" species were amply registered in Argentina (353 records), Costa Rica (341 records) and Chile (161 records) (Figure 1F). The highest observed endemic richness was recorded in Argentina (51 species), Mexico (25 species), and Costa Rica (23 species), and the highest number of "cosmopolitan" species was also recorded in these same countries (66 spp., 39 spp. and 35 spp., respectively). Belize, El Salvador, Guatemala, Guyana, Haiti, Honduras, Jamaica and Panama had no registers for limnoterrestrial and freshwater tardigrades (Figure 1B). The most abundant "cosmopolitan" species were *Macrobiotus hufelandi*, *Milnesium tardigradum*, and *Paramacrobiotus ritchersi*, with 196, 150, and 84 sampling sites, respectively, while *Barbaria bigranulata*, *Mesobiotus coronatus* and *Minibiotus continuus*, with 79, 63 and 62, respectively, were the most frequent endemic ones. Species observed only at their type locality amounted to 66.

Valid species records of non-marine Tardigrada from Andean and Neotropical biogeographic regions, endemic or not, totalized 267 species, of which 186 were found in the Neotropical region (96 endemic and 90 "cosmopolitan"), 105 in the Andean region (43 endemic and 62 "cosmopolitan") and 90 in the Transition Zone (36 endemic and 54 "cosmopolitan"), amounting to 2130 sampling sites (Figure 2A). A total of 139 endemic species corresponded with 715 sites (Figure 2C), while 128 "cosmopolitan" ones were recorded at 1415 sites (Figure 2E). The occurrence of substantial sampling effort for endemic species was noticed in the Guatuso-Talamanca province (112 records), the Puntarenas-Chiriqui province (100 records), and the Guajira province (61 records) (Figure 2D). "cosmopolitan" species were amply registered in the Puntarenas-Chiriqui province (167), the Guatuso-Talamanca province (155) and the Valdivian Forest province (141) (Figure 2F). The highest observed endemic richness was recorded in the Guajira province (21 species), the Valdivian Forest province (19 species), the Puntarenas-Chiriqui, Guatuso-Talamanca and Magellanic Forest provinces (all three with 18 species), and the highest number of "cosmopolitan" species was recorded in the Valdivian Forest province (40 species), the Magellanic Forest (35 species), Atlantic and Puna provinces (both with 30 species). Bahama, Chapada Diamantina, Choco Darien, Comechigones, Ecuadorian, Falkland Islands, Guianan, Imeri, Jamaica, Juan Fernandez, Pará, Roraima, Southern Espinhaço, Trinidad, and Ucayali had no registers for limnoterrestrial and freshwater tardigrades (Figure 2B). Provinces such as Guatuso-Talamanca, Puntarenas-Chiqui, Valdivian Forest, Magellanic Forest, Pampean, and Puna have more sampling sites than all the other 60 provinces. This discrepancy results from the fact that five of these six provinces overlap with countries where most tardigrades were sampled. The most abundant "cosmopolitan" and endemic species in the biogeographical regions were the same as seen for Central and South America.

Figure 3 shows screenshots from the ArcGis online platform of Limnoterrestrial and Freshwater Tardigrada of Central and South America. Four views are depicted here: **A** map view showing all sampling sites included in our dataset, **B** map view showing selected valid endemic species records (blue triangles), **C** map view showing selected valid "cosmopolitan" species records (orange squares), **D** map view showing selected invalid species records due to taxonomical problems (green circles). Each occurrence on the map can be clicked, after which a window with information about the record appears (Fig. 3D). The map can be accessed at https://arcg.is/1jjO84.

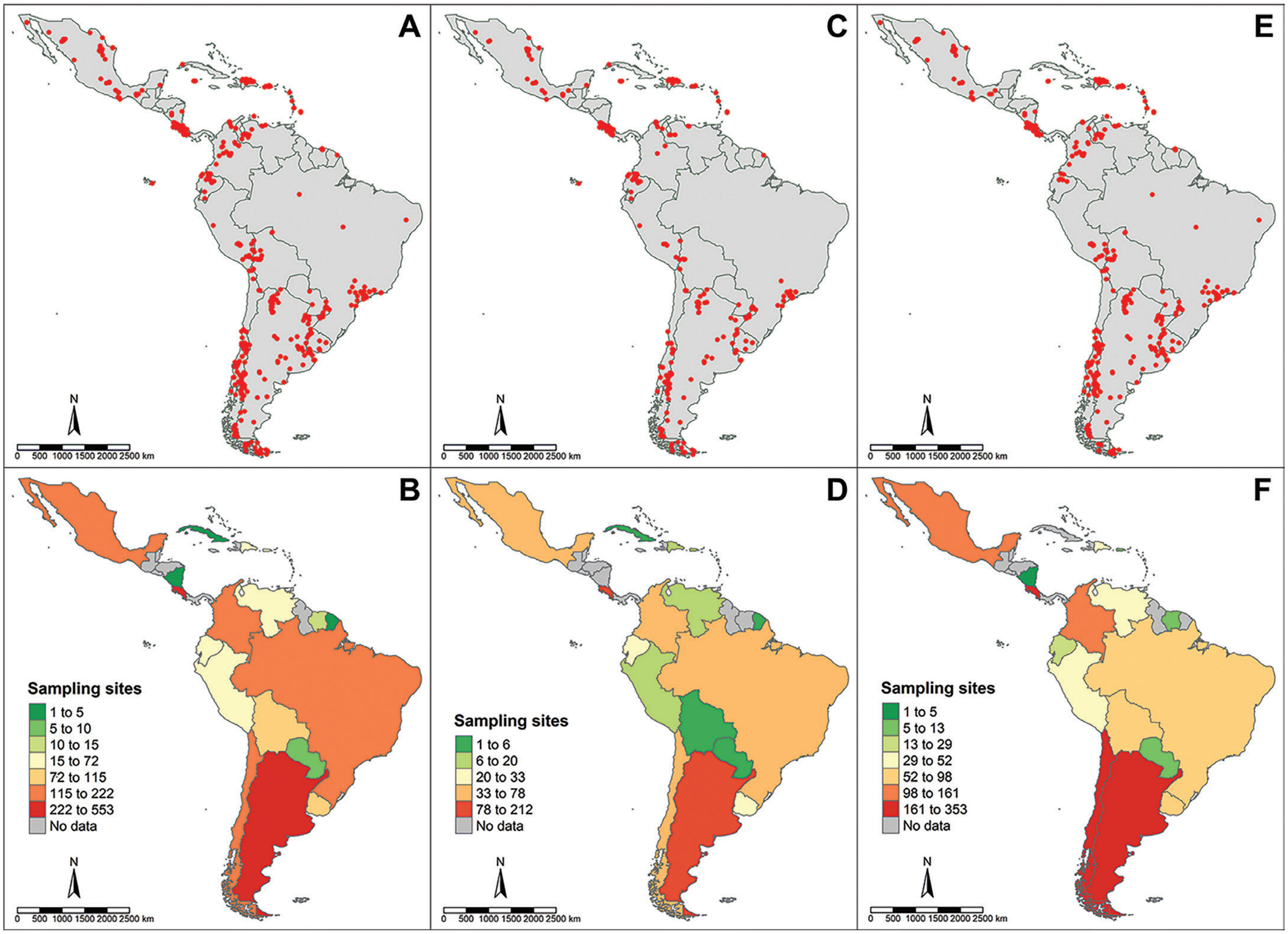

Figure 1. **A** Central and South America map showing the recorded sampling sites (red circles) of limnoterrestrial and freshwater valid tardigrades' species. **B** Documented localities of limnoterrestrial and freshwater valid tardigrades' species in each Central and South American country. **C** Central and South America map showing the recorded sampling sites (red circles) of limnoterrestrial and freshwater valid endemic tardigrades' species. **D** Documented localities of limnoterrestrial and freshwater valid endemic tardigrades' species in each Central and South American country. **E** Central and South America map showing the recorded sampling sites (red circles) of limnoterrestrial and freshwater valid "cosmopolitan" tardigrades' species. **F** Documented localities of limnoterrestrial and freshwater valid "cosmopolitan" tardigrades' species in each Central and South American country.

When analyzing the influence of sampling bias on tardigrade records, we see a positive correlation ($R = 0.78$ and $p < 0.0001$ for countries and $R = 0.77$ and $p < 0.0001$ for biogeographic provinces) between sampling effort and higher observed species richness (Figure 4). Since Argentina is an outlier compared to all other countries and stands out (Figure 4A), it could affect the correlation between variables (Goodwin & Leech 2006). The model was run without Argentina, and the positive correlation was not only maintained, but we obtained a higher value with an even smaller p-value (Figure S1), confirming a consistent pattern in sampling bias.

Discussion

In this study, we demonstrate that general taxonomic literature (e.g., descriptions of new species, checklists, or faunal lists) can be used to create databases that summarize knowledge about species distributions, despite biases caused by predominant taxonomic approaches in each historical period or by the singular view of each researcher (Lewis 1990). These databases contain highly curated registers that are an essential source of information to gain insights into species distributions and diversity patterns (Griffiths et al. 2003, Guénard et al. 2017). Decades or centuries of taxonomic information can be summarized in just one file or website, and records of species occurrences can become publicly available to the scientific community at no cost (Zizka et al. 2019). Furthermore, according to Griffiths et al. (2003), "...when relational databases are linked to a Geographical Information System (GIS), they become an even more powerful tool for taking on large-scale biogeographical patterns".

Critical evaluation of the historical and contemporary tardigrade records is of utmost importance to understand this taxon's phylogenetic diversity and distribution patterns around the globe (Morek et al. 2019). Most of the records in our dataset (1425 out of 2157) are from so-called "cosmopolitan" species and date to a period (early and middle 20th century) when the widespread distribution of many tardigrades

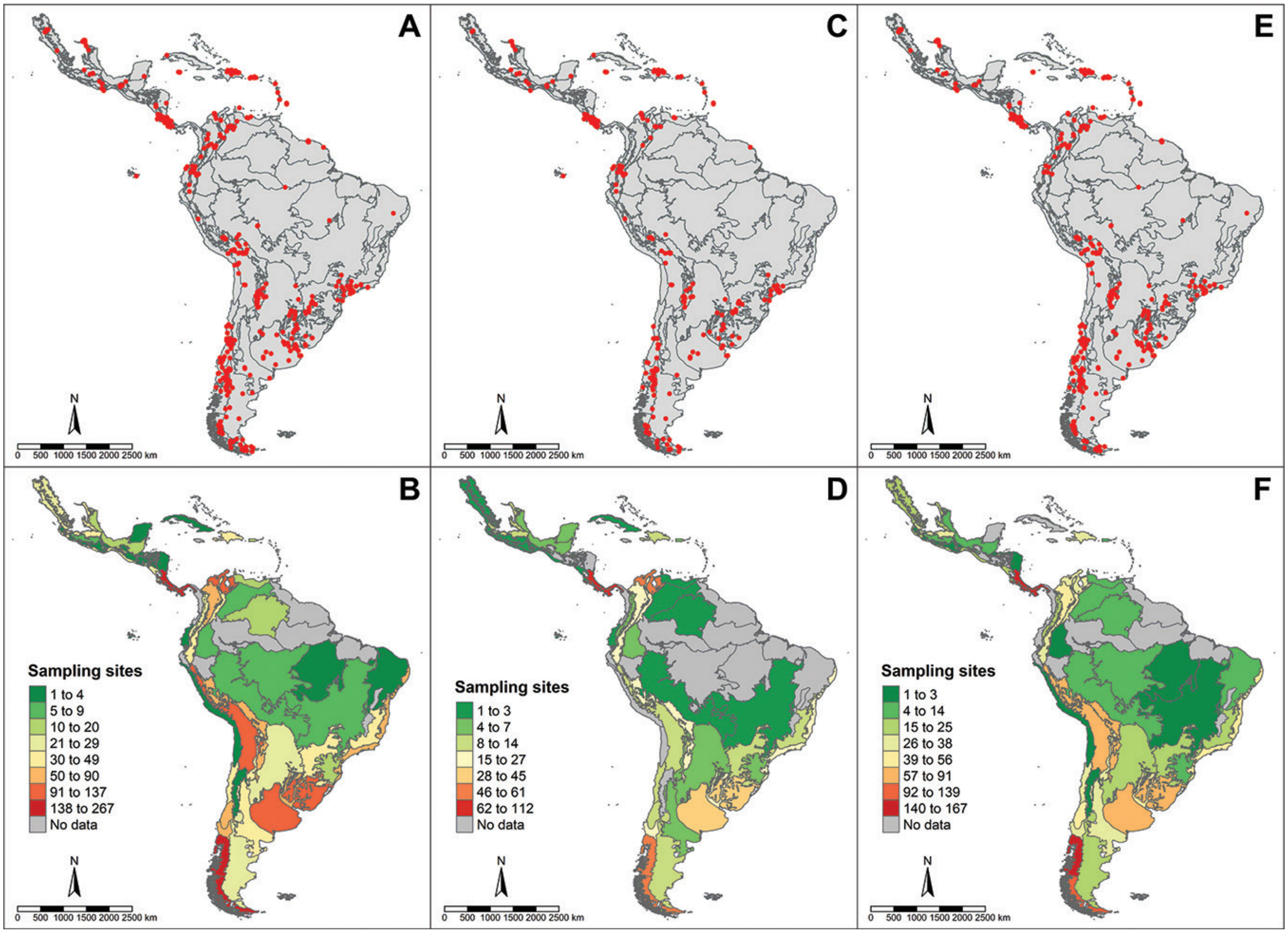

Figure 2. A Neotropical and Andean biogeographic regions' map with the recorded sampling sites (red circles) of limnoterrestrial and freshwater valid tardigrades' species. **B** Documented localities of limnoterrestrial and freshwater valid tardigrades' species in each biogeographic province of the Andes and Neotropical regions. **C** Neotropical and Andean biogeographic regions' map with the recorded sampling sites (red circles) of limnoterrestrial and freshwater valid endemic tardigrades' species. **D** Documented localities of limnoterrestrial and freshwater valid endemic tardigrades' species in each biogeographic province of the Andes and Neotropical regions. **E** Neotropical and Andean biogeographic regions' map with the recorded sampling sites (red circles) of limnoterrestrial and freshwater valid "cosmopolitan" tardigrades' species. **F** Documented localities of limnoterrestrial and freshwater valid "cosmopolitan" tardigrades' species in each biogeographic province of the Andes and Neotropical regions.

was broadly accepted. One emblematic case regarding this thought is *Milnesium tardigradum* Doyerè, 1840, which was considered ubiquitous for decades (Morek et al. 2021). In our study it was the second species with the highest number of records among all 271 species and was found in 15 countries in both regions. This view changed only recently when Michalczyk et al. (2012) and Morek et al. (2019) applied an integrative approach to redescribe and better understand the intraspecific variability in *M. tardigradum* and when Tumanov et al. (2022) found that the distribution of this species is restricted to the Paleartic region. Together with *M. tardigradum*, many other widespread species (e.g., *Macrobiotus hufelandi*, *Paramacrobiotus ritchersi*, *Minibiotus intermedius*, *Pseudechiniscus (Pseudechiniscus) suillus*) were described in the late 19th or early 20th centuries, which means that taxonomic problems may arise due to incomplete descriptions, lack of type series deposited in zoological Museums and/or the non-use of modern techniques for morphological analyses. Thus, most species identification and records should be considered dubious or invalid (Michalczyk et al. 2012, Morek et al. 2019, Gąsiorek et al. 2021). Despite that, many tardigrade species' definitive distribution range is far from known, the "EiE" hypothesis does not explain the wide geographic distribution of many of them. However, although it is not simple to distinguish natural and human-mediated dispersal, Gąsiorek et al. (2019a, b) extend the discussion regarding the latter, proposing human's pivotal role in the dispersal of some tardigrade species worldwide.

We plotted records on countries' geopolitical/administrative boundaries as well as biogeographical regions, mapping geographical areas categorized according to their climatic, geological, and biota (including endemic taxa) criteria (Escalante et al. 2009, Morrone 2015a, Morrone 2015b, Morrone 2017, Morrone et al. 2017, Morrone 2018, Morrone et al. 2022), in Central and South America (Andean and Neotropical regions). When studying species distribution and diversity

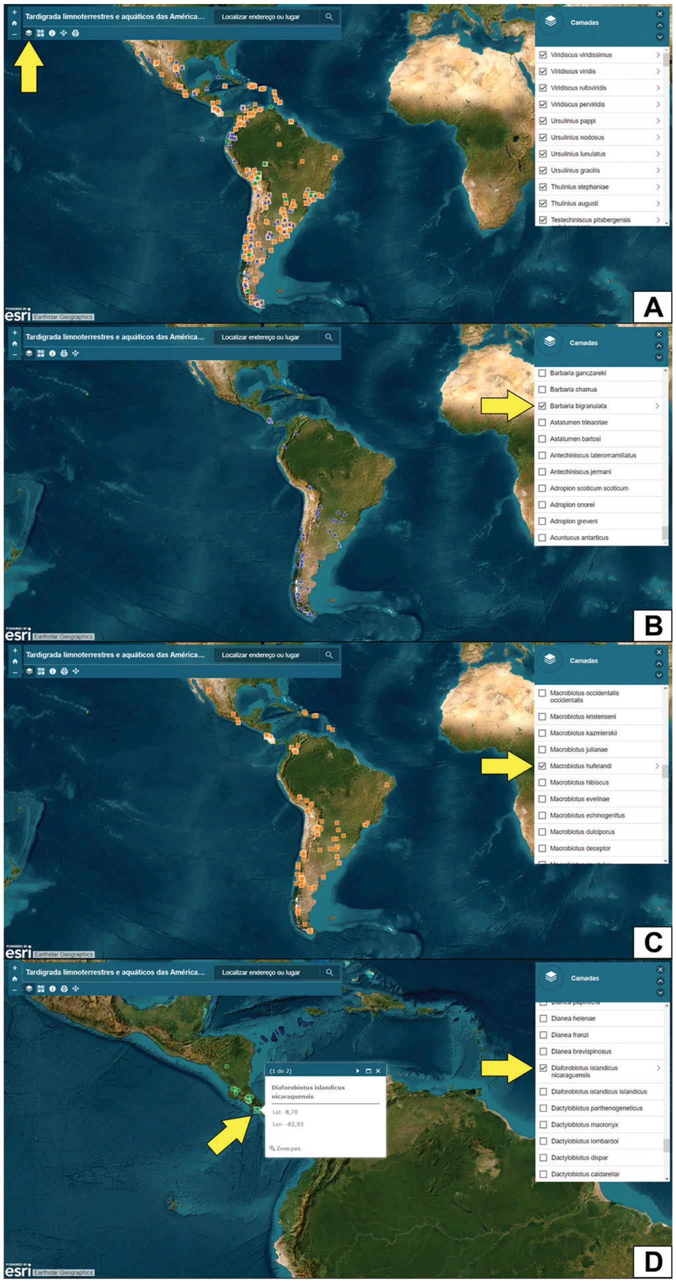

Figure 3. **A** All available sampling sites. **B** Selected record of *Barbaria bigranulata* Ritchers, 1907 (valid endemic species). **C** Selected records of *Macrobiotus hufelandi* C.A.S. Schultze, 1834 (valid "cosmopolitan" species). **D** Selected records of *Diaforobiotus islandicus nicaraguensis* Seméria, 1985 (taxonomically invalid) and associated information is shown when a record is clicked on.

patterns, a widely used method considers geopolitical/administrative boundaries valid units (Murphy 2021), however they rarely concur with ecological boundaries, as they are constantly subject to changes (Wilson & Donnan 2012). Murphy (2021) demonstrated several critical issues of this practice, which include overestimating endemism, underestimating biodiversity metrics (particularly endemism estimates), hindering understanding of biodiversity discontinuity across the world (especially true for measures containing species range size), and identifying hotspots. Thus, biogeographic regionalization is essential to comprehend ecological and evolutionary aspects of life (Crisp et al. 2009, Holt et al. 2013, Flores-Tolentino et al. 2021).

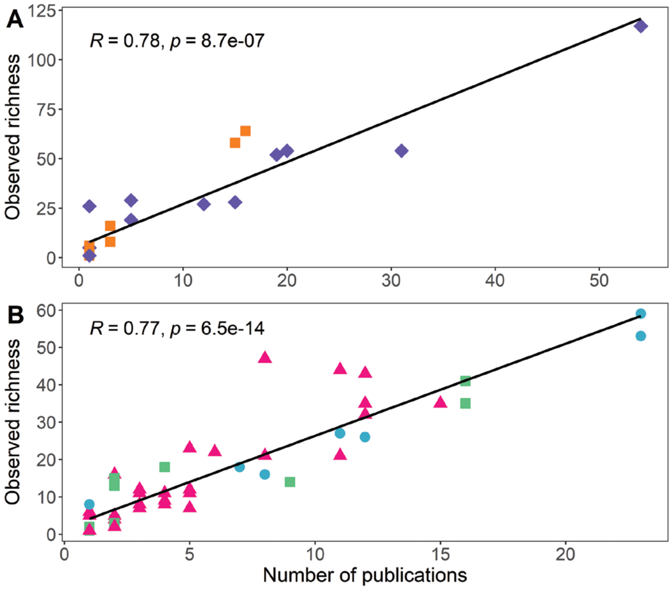

Figure 4. **A** Correlation between the number of published articles and known valid species richness for each country. Orange squares represent Central American countries, while purple diamonds represent South American ones. There are overlapping data represented in the chart. Countries with zero published papers (Belize, El Salvador, Guatemala, Guyana, Haiti, Honduras and Panama) were excluded. Kendall Rank's Rvalue correlation and p-value are shown in the upper left corner. **B** Correlation between the number of published papers and known valid species richness for each biogeographic province. Pink triangles represent Neotropical biogeographic provinces, while blue circles represent Andean and green squares Transition zone provinces. There are overlapping data in the chart. Provinces with zero published papers (Bahama, Chapada Diamantina, Choco Darien, Comechigones, Ecuadorian, Falkland Islands, Guianan, Imeri, Jamaica, Juan Fernandez, Pará, Roraima, Southern Espinhaço, Trinidad, and Ucayali provinces) were excluded. Kendall Rank's R correlation and p-value are shown in the upper left corner.

The Andean and Neotropical regions are hierarchically arranged in five levels: kingdoms, regions, dominions, provinces, and districts (Morrone 2015b), meaning they do not represent countries' political boundaries. However, countries with considerable sampling effort and intensity will translate to provinces with more sampling sites and higher observed richness (Figure 4), as seen in this study. Due to a sampling bias, this phenomenon is known as the "specialist" effect, where distribution data explains who is researching these organisms instead of their actual distribution (Fontaneto et al. 2012). Argentina is a clear example of this statement, as it was ranked second in the total number of records and first in observed richness. The substantial sampling effort in this country was enough to consider it an outlier in our analysis and removing it from the statistical analysis yields a higher positive correlation (Figure S1). Thus, Argentina outperforms all other countries in Central and South America regarding the relationship between observed richness and published articles. Another case would be Costa Rica. The country already had studies of tardigrade ecology conducted there (Mehlen 1969, Kaczmarek et al. 2011, Stander 2016), justifying why it is the first and third country in overall sampling sites and observed richness. Consequently, overlapping biogeographical provinces with both countries will have higher observed richness due to substantial localized sampling effort (e.g., Guatuso-Talamanca and Puntarenas-Chiriqui provinces with Costa Rica).

Finally, studying species' large-scale distribution patterns is not a simple task for meiofaunal organisms, especially in the Southern Hemisphere (Fontaneto et al., 2012, Garraffoni et al., 2021), because of significant sample bias and predominantly Eurocentric sampling (Guil & Cabrero Sañudo 2007, Schill 2018). The "meiofaunal paradox" (Giere 2008), while supposedly adhering to the "EiE" hypothesis (Finlay et al. 1996, Fenchel et al. 1997, Fenchel & Finlay 2004), does not help with the current shortfalls (Linnean and Wallacean) to explain how these organisms were able to colonize multiple habitats. Moreover, consolidating historical non-marine tardigrade records without a thorough taxonomical analysis, especially with an integrative approach, only hinders advancements in comprehending the diversity, biogeography, and evolution of limnoterrestrial tardigrades (Morek et al. 2019, Gąsiorek et al. 2019a, Gąsiorek et al. 2021). Albeit, historically, little investigation was done to understand tardigrade habitat patterns (Guil et al. 2009), there has been a growing body of evidence showing there are limits to their distribution (Guil et al. 2009, Mogle et al. 2018, Morek et al. 2019, Gąsiorek et al. 2019a, Morek et al. 2021, Garraffoni et al. 2021, Tumanov et al. 2022).

This database and the online interactive map will significantly help future studies on limnoterrestrial and freshwater tardigrades' biogeography and ecology in Central and South America. Although we have provided valuable insights into certain areas of knowledge of these organisms, their study continues to face obstacles due to numerous critical deficiencies that remain unresolved. We believe that implementing a more homogenous and widespread sampling across both regions and performing analyses of all specimens utilizing an integrative taxonomic approach will greatly benefit the understanding of the diversity and distribution patterns of limnoterrestrial and freshwater tardigrades.

Supplementary Material

The following online material is available for this article:

Table S1 - List of publications from 2014 to 2023 on limnoterrestrial and freshwater Tardigrada from Central and South America.

Table S2 - List of species with their respective taxonomical issue(s) and reference(s) for species of non-marine tardigrades from Central and South America according to Degma & Guidetti (2023).

Figure S1 - Correlation between the number of published articles and known species richness for each country (excluding Argentina). Orange squares represent Central American countries, while purple diamonds represent South American ones. There are overlapping data represented in the chart. Countries with zero published papers (Belize, El Salvador, Guatemala, Guyana, Haiti, Honduras and Panama) were excluded. Pearson's R-value correlation and p-value are shown in the upper left corner.

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Author Contribution

Pedro Danel de Souza Ugarte: substantial contribution to the concept and design of the study; data collection; analysis and interpretation; manuscript preparation and critical revision, adding intellectual content.

Luisa Pucci Suzuki: data collection, analysis, and interpretation; manuscript preparation.

Laura Gonsalves Cruvinel: data collection, analysis, and interpretation.

André Rinaldo Senna Garraffoni: substantial contribution to the concept and design of the study; analysis and interpretation; manuscript preparation and critical revision, adding intellectual content.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data Availability

The dataset generated during the current study is available at: https://doi.org/10.48331/scielodata.JQJBE9

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