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BIOLOGICAL SCIENCES

Reproductive biology of *Erythrolamprus jaegeri coralliventris* (Serpentes: Dipsadidae) in the Brazilian Coastal Pampa

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Abstract: We analyzed reproductive biology of *Erythrolamprus jaegeri coralliventris*, a snake from the Brazilian Pampa. Females presented larger snout-vent length than males, while no significant differences were found in tail length/snout-vent length ratios between sexes. Females attain sexual maturity in larger sizes than males. The reproductive cycle of females presented a seasonal pattern, with advanced vitellogenesis occurring from middle winter to middle spring and oviductal eggs occurring from middle winter to middle summer. The real fecundity ranged from two to eigth eggs and the expected fecundity varied from one to 12 secondary follicles. No significant correlation was found between females body size and the following parameters: real fecundity, length of the largest egg and potential fecundity. Therefore, *E. j. coralliventris* presents a seasonal reproductive pattern, which seems to follow the rainfall profile observed for the studied region. This may represent a strategy of energy gain associated to the reproductive cycle, considering that the food resources most explored by this species are anurans that present higher activity during rainy periods.

Key words: fecundity, seasonality, sexual dimorphism, sexual maturity, Xenodontinae.

INTRODUCTION

Erythrolamprus Boie 1826 *sensu lato* is one of the most diverse genera of Neotropical dipsadids, comprising 50 species of small to medium-sized oviparous snakes, widely distributed in Central and South America, as well as the Antilles archipelago (Dixon 1989, Lema 2002, Uetz & Hošek 2018). The Jaeger's Ground Snake *Erythrolamprus jaegeri* Günther 1858 is a small-sized semi-aquatic species, included in the *Erythrolamprus typhlus* group (Dixon 1987). In the coastal region of southern Brazil, *E. jaegeri* is the one of the most abundant snake species (Quintela & Loebmann 2009). Two subspecies are recognized, the nominal *E. j. jaegeri* and *E. j. coralliventris* (Dixon 1987).

Erythrolamprus jaegeri coralliventris is the southernmost distributed subpecies, ranging from Paraguay to Argentina (Giraudo 2001, Uetz & Hošek 2018). *Erythrolamprus jaegeri coralliventris* inhabits mainly open areas near to water bodies (Quintela & Loebmann 2009) and feeds preferentially on small anurans, although it may occasionally preys on fish, small lizards and insects (Carreira-Vidal 2002, Corrêa et al. 2016).

Studies describing aspects of the reproductive biology of the genus *Erythrolamprus* are still scarce (e.g. Vitt 1983, Marques 1996, Pinto & Fernandes 2004, Pizzatto & Marques 2006a, b, López et al. 2009, Prieto et al. 2012, Quintela et al. 2017, Rojas et al. 2017). However, knowledge about the reproductive aspects of species represents an useful tool for understanding evolutionary strategies in the natural history of snakes, since the perpetuation of a species is a result of the reproductive success (Seigel & Ford 1987). In the temperate zone regions, the reproductive cycle of snakes tends to be limited by temperature variations caused by seasonality (Shine 1985). Therefore, one can *a priori* assume that environmental variables such as temperature, precipitation and other present different effects over the reproductive activity of snake species. Within this context, snakes from genus *Erythrolamprus* can use different reproductive strategies as adaptations to environmental factors, such as the synchronization of reproductive cycle and the period of higher prey availability (Vitt 1983, Marques 1996, Pinto & Fernandes 2004) and the occurrence of constraints imposed by thermal requirements (Pizzatto & Marques 2006a, Quintela et al. 2017). Bellini et al. (2016), however, indicate that phylogenetic relationships are more determinant in the reproductive cycle in Xenodontinae snakes than ecological factors. Thus, different xenodontine species may have reproductive patterns controlled by evolutive or environmental factors.

Aspects of reproduction of *E. jaegeri* were investigated across a wide latitudinal range, covering population from tropical and subtropical climatic domains (J.G. Frota, unpublished data). Here in, we analyzed the reproductive biology of *Erytholamprus jaegeri coralliventris* in the Pampa biome, in subtropical domains of southern Brazil. We examined sexual dimorphism, reproductive cycle in females, fecundity and size at sexual maturity. In view of the seasonal pattern found in all dipsadids so far studied in subtropical domains of Pampa biome and surrounding Atlantic Forest (Aguiar & Di-Bernardo 2005, Balestrin & Di-Bernardo 2005, Zanella & Cechin 2010, Mesquita et al. 2013, Panzera & Maneyro 2013, Rebelato et al. 2016, Loebens et al. 2016, 2017, Quintela et al. 2017), we hypothesize that *E. j. coralliventris* will also exhibit a reproductive pattern characterized by marked seasonality.

MATERIALS AND METHODS

We analyzed 298 specimens of *Erythrolamprus jaegeri coralliventris* collected between 2008 and 2016 in the municipalities of Pelotas, Rio Grande and São José do Norte, all of them located at state of Rio Grande do Sul, Southern Brazil (31°42’29”S - 32°32’25”S, 52°32’21”W - 51º55’05”W). All specimens are deposited in the Herpetological Collection of Universidade Federal do Rio Grande (CHFURG) (Appendix). The study area is inserted in the Pampa biome (IBGE 2004). The seasons are well marked and rainfall is concentrated mainly in winter and spring (Vieira 1984). The monthly averages of air temperatures and fluvial discharge (rainfall estimates) of the study area over the sampling period are shown in Figure 1. The predominant vegetation type are shrub grasslands; other phytophysiognomies with less coverage include the coastal peat and sandy forests (*restinga* forests), and the psammophyte formations of coastal dunes. All procedures adopted are in accordance with the institutional committee on ethics in the use of animals for research.

We determined the sex of specimes through a subcaudal incision and inspecting the presence or absence of a hemipenis. The measurements of snout-vent length (SVL), tail length (TL) and tail proportion in relation to SVL (TL/SVL ratio) were obtained from all specimens. Males were considered mature when showing ductus deferens coiled and opaque, which indicates the presence of sperm (Shine 1977, Almeida-Santos et al. 2014). Females were considered

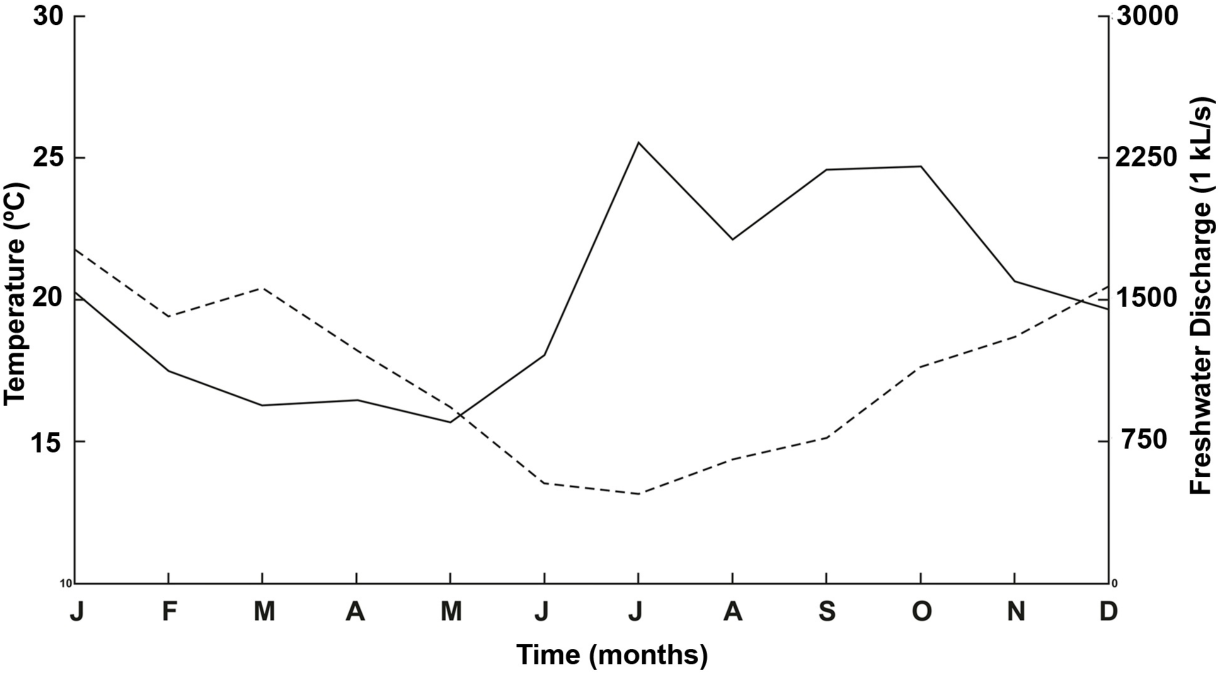

Figure 1. Monthly means (grouped months) profiles of air temperatures (dashed line) and fluvial discharge (rainfall average estimates; straight line) obtained between January 2009 and August 2016 in the study area.

sexually mature when presenting at least one of the following characteristics: 1) presence of secondary follicles; 2) presence of eggs in the oviducts; 3) presence of emptied incubation chambers, which indicates a recent oviposition (Blackburn 1998). We verified the existence of significant differences in the SVL of mature males (n=107) and females (n=124) through a *t* text (significance $p < 0.05$). The existence of significant differences in the proportion of tail in relation to body length between mature males (n=107) and females (n=124) was examined through an ANCOVA (Analysis of Covariance), using SVL as the covariate (significance $p < 0.05$) (Aguiar & Di-Bernardo 2005, Mesquita et al. 2013). All database was previously checked for normal distribution through Shapiro-Wilk test (p values between 0.0000123 and 0.0019).

In all specimens, we made a ventral incision from the esophageal to around 3 mm above the cloaca and the reproductive tract was externalized for analysis. The following data were obtained from females: 1) total number of ovarian follicles, 2) number of follicles in secondary vitellogenesis (secondary follicles; largest axis ≥ 5 mm, based on the annual scatterplot profile of the largest folicle of females; see Almeida-Santos et al. 2014), 3) length of the largest axis of the largest ovarian follicle, 4) total number of eggs, 5) length of the largest egg. In order to identify seasonal variation on follicle development, the length of the the largest axis of the largest follicles of each female were plotted on a graph (Almeida-Santos et al. 2014). Fecundity was obtained based on the number of eggs in the oviduct (real fecundity) and number of secondary follicles (potential fecundity) (Mesquita et al. 2013). Through a Pearson correlation test, we verified the existence of correlation between SVL and the following parameters: 1) total number of eggs, 2) length of the largest egg, 3) number of secondary follicles Statistical analyses were performed in the software PAST v.2.17 (Hammer et al. 2013).

RESULTS

We analyzed a total of 298 specimens, 155 males (107 mature, 48 immature) and 143 females (124 mature, 19 immature). The SVL of mature males ranged from 185 to 396 mm (mean [*X*] = 310 mm, standard deviation [*sd*] = 53 mm). The SVL of mature females ranged from 245 to 480 mm (*X* = 345 mm, *sd* = 52 mm). The TL/SVL ratio in males ranged from 0.170 to 0.495 (*X* = 0.286, *sd* = 0.035) while in females this ratio ranged from 0.158 to 0.375 (*X* = 0.285, *sd* = 0.026). The *t* test showed a significant difference in SVL between sexes (*p* = 0.0000824; *t* = 3.99), while the ANOVA detected no significant diference between tail proportions in relation to SVL (*p* = 0.84; F = 0.036).

Females presented primary follicles throughout all months of the year. Secondary follicles occurred between late autumn and early summer, although a marked increase in diameter was observed from middle winter to middle spring (Figure 2). Eggs were found in 17 females, sampled between middle winter and middle summer. The number of eggs (real fecundity) ranged from 2 to 8 (*X* = 6.64, *sd* = 1.65). The number of secondary follicles (potential fecundity) ranged from 1 to 12 (X = 6.72; *sd* = 3). The smallest female with secondary follicles had SVL = 320 mm while the smallest female with

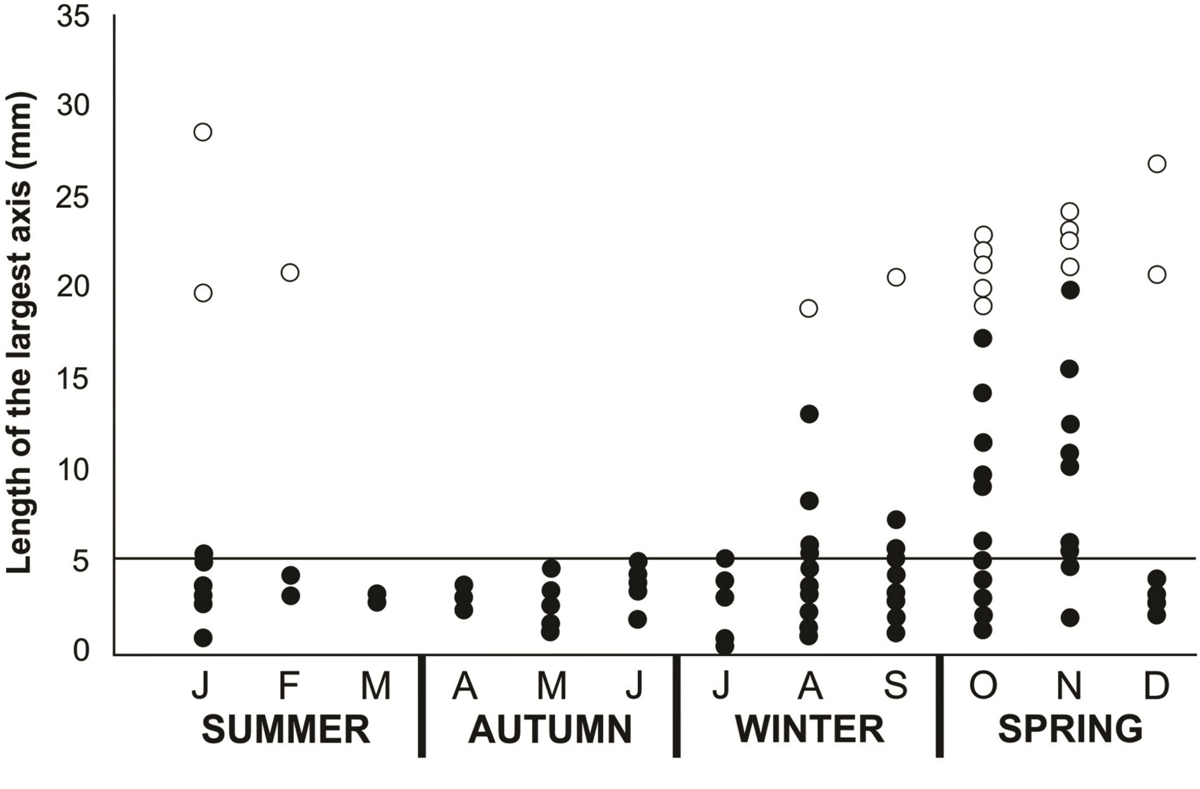

Figure 2. Monthly variation in the length of the largest axis of the largest follicles (black circle) and eggs (white circle) of *Erythrolamprus jaegeri coralliventris* from Brazilian coastal Pampa, state of Rio Grande do Sul. The horizontal line represents the length of the largest axis from which the follicles are considered in secondary vitellogenesis (5 mm).

eggs presented SVL = 245 mm. A single female carrying eggs (n=8) presented seccondary follicle (n=1; length = 10.89 mm). No significant correlation was found between SVL and number of eggs (*r* = 0.10, *p* = 0.68), SVL and the length of the largest egg (*r* = 0.30, *p* = 0.24) and SVL and number of secondary follicles (*r* = 0.16, *p* = 0.63).

DISCUSSION

Our results indicated that *E. j. coralliventris* females attained larger body size (SVL) than males, corroborating data from *E. j. jaegeri* (J.G. Frota, unpublished data) and other xenodontines (e.g. Aguiar & Di-Bernardo 2005, López & Giraudo 2008, Orofino et al. 2010, Zanella & Cechin 2010, Mesquita et al. 2013, Panzera & Maneyro 2013, Rebelato et al. 2016). This pattern is commonly observed in snakes that do not present male-to-male combat (Shine 1994). The larger body size in females represents an adaptation associated to its reproductive success, considering that body size is related to fecundity and size of eggs/embryos (Pizzatto et al. 2007, Mesquita et al. 2013). In our study, however, we did not verify a significant correlation between female body size (SVL) and fecundity, indicating that other aspect could be related to the female-biased sexual dimorphism in size. Shine (1994) analyzed 374 species from eigth families and found that phylogenetic conservatism represented the main driving force acting on sexual size dimorphism (SSD) in snakes, while fecundity selection did not correlate significantly with SSD. Female-biased SSD was also observed in other *Erytrolamprus* studied species (Marques et al. 1996, Pizzatto & Marques 2006b, López et al. 2009, Prieto et al. 2012, Quintela et al. 2017), corroborating the occurrence of phylogenetic conservatism in SSD within the genus.

Mature males and females of *E. j. coralliventris* are respectively slightly smaller than mature males and females of *E. j. jaegeri* (J.G. Frota, unpublished data) and in both subspecies females attain sexual maturity in greater sizes than males. The greater size of females at sexual maturation was also demonstrated in all previous studies approaching this aspect on Dipsadidae (e.g. Aguiar & Di-Bernardo 2005, Zanella & Cechin 2010, Panzera & Maneyro 2013, Rebelato et al. 2016, Quintela et al. 2017). The delay in sexual maturity in females until reaching larger sizes becomes an advantageous reproductive strategy, considering that it should result in larger accomodation for offsprings (Panzera & Maneyro 2013). The absence of significant differences between tail proportions in males and females, on the other hand, was not expected, considering that the hemipenis and associated retractor musculature are placed in the caudal segment of males (King 1989). No significant differences were found in tail proportions between sexes of *L. j. jaegeri* (J.G. Frota, unpublished data) while the congener *E. poecilogyrus* exhibited a geographic variation in relation to tail ratios between sexes (see Quintela et al. 2017). Among dipsadids, there is a clear tendency for relatively longer tails in males (see Aguiar & Di-Bernardo 2005, Pizzatto et al. 2008, Orofino et al. 2010, Panzera & Maneyro 2013, Mesquita et al. 2013) but there are also cases of absence of significant differences in tail proportions between sexes, as observed in *Echinanthera cyanopleura* (Zanella & Cechin 2010) and *Imantodes cenchoa* (Sousa et al. 2014). A possible explanation for the lack of male-biased sexual dimorphism in tail proportion of our *E. j. coralliventris* sample could be related to the relationships between fecundity and body size (SVL). According to King (1989), when fecundity is correlated to (SVL), shorter tails in females take place as a secondary result of the increased reproductive capacity (natural selection for increased SVL). Once no significant correlation was found between SVL and fecundity, it is conceivable that secondary effects of SVL proportion on tail length is few pronounced in our *E. j. coralliventris* female sample, resulting in little contrast between male and female TL proportions.

As postulated by our previous hypothesis, *E. j. coralliventris* populations from the southernmost Brazilian coast exhibits a seasonal reproductive pattern, as seen by the female cycle. This finding corroborates data from the great majority of investigations on dipsadids at the subtropical ecoregions of Pampa and southern Atlantic Forest (Aguiar & Di-Bernardo 2005, Balestrin & Di-Bernardo 2005, Zanella & Cechin 2010, Mesquita et al. 2013, Panzera & Maneyro 2013, Rebelato et al. 2016, Loebens et al. 2017, Quintela et al. 2017). The females of *E. j. coralliventris* herein studied presented a marked seasonality in advanced vitellogenesis and egg production, which extended from middle winter to middle summer (Figure 2). This pattern demonstrates that low temperatures during winter do not limit the advanced vitellogenesis and egg production. Meanwhile, the peak of secondary vitellogenesis is associated with inscreasing temperatures in spring, which indicates that female reproductive cycle is strongly influenced by temperature, in accordance with the typical subtropical pattern (Mathies 2011). Further, the pattern of vitellogenic growth seems to follow the rainfall profile, which in the study area increases considerably in the beginning of winter and remains relatively higher until early summer (Figure 1). Thus, the reproductive cycle of females seems to be restricted to the period of higher precipitation. This fact can be related to the food resources explored by *E. j. coralliventris*, consisting mainly of anuran amphibians (Corrêa et al. 2016) which are more active during rainy periods (Santos et al. 2008). Therefore, this synchrony between the reproductive cycle and the rainy season (the last presumably related to an increase on prey availability) becomes advantageous, since snakes do not start their reproductive cycle until they have enough energy to support the required metabolic costs (Bonnet et al. 1998). In several snake species, females request higher energy investment in order to initiate its reproductive cycle (Seigel & Ford 1987). Females of *E. j. jaegeri* also exhibited a seazonal reproductive cycle (J.G. Frota, unpublished data), but a longer period of secondary vitellogenesis and a shorter period of egg production was observed in relation to our *E. j. coralliventris* sample. Meanwhile, specimens of *E. j. jaegeri* analyzed by J.G. Frota (unpublished data) were distributed in both tropical and subtropical climatic domains, which limits further comparisons and discussions.

Erythrolamprus jaegeri coralliventris herein analyzed presented the same range of potential fecundity than *E. j. jaegeri* (J.G. Frota, unpublished data) while real fecundity was slightly higher in the later. No significant correlation was observed between SVL and fecundity parameters, and SVL and egg size in our *E. j. coralliventris* sample. The absence of correlation between SVL and litter size was also verified for *E. j. jaegeri* (J.G. Frota, unpublished data) and congener *E. poecilogyrus* (Pinto & Fernandes 2004, Quintela et al. 2017), corroborating with our results. Studies performed with other xenodontine species, however, showed a positive correlation between SVL and litter size, but not when SVL and egg size were compared (e.g. Marques 1996, Pizzatto & Marques 2002, Pizzatto et al. 2008, Panzera & Maneyro 2013). These relationships, therefore, seem to be variable and intrinsic in Xenodontinae species. The presence of a unique secondary follicles in a single females carrying eggs in our *E. j. coralliventris* sample also indicates that only one litter per reproductive period can be produced, which contrasts with sympatric/syntopic *E. poecilogyrus sublineatus* (Quintela et al. 2017).

In the present study we observed that *Erythrolamprus jaegeri coralliventris* from Brazilian coastal Pampa presents a seasonal reproductive pattern, possibly influenced by climatic and ecological factors (rainfall and its effects on the availability of food resources). In this context, it is suggested the conduction of studies on the reproductive biology of *Erythrolamprus jaegeri* in other climatic domains, in order to clarify how environmental, ecological and phylogenetic factors affect the reproduction of the species.

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APPENDIX

Specimens examined from the herpetological collection of Universidade Federal do Rio Grande (CHFURG): Brasil: Rio Grande do Sul: Pelotas (CHFURG 4635, 4642, 4644, 4645, 4646, 4647, 4648, 4692, 4693, 4774, 5722); Rio Grande, Ilha do Leonídeo (CHFURG 4638, 4667, 4669), Parque Marinha (CHFURG 931), Senandes (CHFURG 1023, 1027, 1028, 1034, 1254, 1258, 1261, 1262), Área de Proteção Ambiental da Lagoa Verde (CHFURG 1577, 1580, 1586, 1590, 1592, 1593, 1594, 1596, 1599, 1602, 1605, 1648, 1651, 1652, 1655, 1664, 1720, 1785, 1790, 1795, 1796, 1798, 1803, 1805, 1806, 1807, 1809, 1813, 1817, 1824), Barra (CHFURG 3265), Bolaxa (CHFURG 1939, 3086, 3095, 3146, 3147, 3148, 3149, 3150, 3264, 3265), Cassino (CHFURG 1081, 1082, 1083, 1084, 1085, 1086, 1087, 1088, 1089, 1090, 1091, 1092, 1582, 1589, 1649, 1778, 1950, 5228, 5470, 5474, 5486, 5493, 5499, 5603), *Campus* da Universidade Federal do Rio Grande – FURG (CHFURG 1583, 1940, 2821, 2911, 2912, 2912, 2974, 2974, 2991, 2993, 2994, 2995, 3238, 3238, 4670, 4715), Distrito Industrial da Barra (CHFURG 1576, 1578, 1587, 1595, 1606, 1647, 1650, 1653, 1654, 1656, 1797, 1801, 1808, 1814, 1935, 1936, 2018, 2960, 2970, 2973, 3084, 3085, 3086, 3087, 3092, 3093, 3094, 3096, 3210, 3253, 3262, 3263, 3271, 3272, 3304, 3307, 3308, 3309, 3310, 3311, 3312, 3313, 3314, 3315, 3316, 3317, 3318, 3319, 3333, 3334, 3335, 3336, 3337, 3338, 3375, 3376, 3377, 3378, 3434, 3995, 3996, 3997, 3998, 3999, 4000, 4001, 4002, 4003, 4004, 4005, 4006, 4007, 4008, 4009, 4010, 4011, 4012, 4013, 4014, 4042, 4043, 4044, 4045, 4046, 4047, 4048, 4049, 4050, 4051, 4402, 4406, 4414, 4422, 4423, 4424, 4425, 4430, 4431, 4432, 4433, 4434, 4435, 4436, 4437, 4438, 4439, 4440, 4441, 4634, 4636, 4637, 4639, 4649, 4651, 4652, 4654, 4653, 4655, 4656, 4657, 4658, 4659, 4660, 4661, 4662, 4664, 4672, 4673, 4675, 4676, 4677, 4678, 4681, 4682, 4683, 4684, 4685, 4690, 4695, 4696, 4698, 4699, 4735, 4736, 4737, 4739, 4793, 4794, 4795, 4806, 4807, 4838, 4839, 4840, 4892, 4903, 4915, 4916, 4917, 4984, 4992, 4999, 5000, 5001, 5061, 5085, 5062, 5365, 5590), Estação Ecológica do Taim (CHFURG 1077, 1271, 1272, 1736, 2506, 3241, 3242, 3243, 3244, 3562, 4717); São José do Norte (CHFURG: 5722, 5723).

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Author contributions

VHST collected specimens (in part), prepared material, analyzed data and wrote first manuscript draft. FMQ collected specimens (in part) and help in manuscript preparation. DL coordinate this research, edited manuscript style and format, besides of have submitted manuscript to AABC journal.