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The high diversity and phylogenetic signal of antipredator mechanisms of the horned frog species of *Proceratophrys* Miranda-Ribeiro, 1920 (Amphibia: Anura: Odontophrynidae)

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Abstract. Phylogenetic signals indicate the phenotypic similarity of antipredator mechanisms among related species. Herein, we assessed the antipredator mechanisms of the horned frog *Proceratophrys laticeps*, compiled a database including closely phylogenetically-related species, and evaluated their phylogenetic signals. Our dataset comprises 80 records for 13 species of *Proceratophrys*, totalizing 11 antipredator mechanisms and 15 variations of these mechanisms. Six antipredator mechanisms show high similarity in the trees' roots within *Proceratophrys* (e.g., aggression, aposematism, camouflage, distress call, immobility, and interrupt calling). Our observations show the first records of antipredator mechanisms for *P. laticeps*, and the first report of interrupt calling for *Proceratophrys* genus, contributing to the knowledge on the behavioural ecology of *Proceratophrys* species, addressing new insights for ecological trait evolution by multiple ancestral states of amphibians.

Keywords. Ancestral trait, anurans, Brownian motion, defensive strategies, evolution, phylogenetic tree.

Observations from closely phylogenetically-related species are often statistically non-independent due to common ancestry (Felsenstein, 1985; Harvey and Pagel, 1991). Shared history leads to the phenotypic similarity among related species under many evolutionary processes (Hansen and Martins, 1996). This phylogenetic dependence in the data can be accounted using various special statistical methods developed for phylogenetic data (e.g., Felsenstein, 1985; Hansen and Martins, 1996; Rohlf, 2001). Phenotypic similarity among related species is known as phylogenetic signal and describes the tendency of a particular characteristic to be conserved (Blomberg and Garland, 2002). The degree of phylogenetic signal can indicate the weight to which closely related species tend to have similar traits (Blomberg et al., 2003). Phenotypic traits may depend upon for root of a phylogenetic tree or may converge to their tips (Paivone et al., 2010). Moreover, the evolution of these characteristics can be explained by Brownian motion, a process of random genetic drift at a constant rate of evolution and non-directional selection (Diniz-Filho and Vieira, 1998).

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Predation is probably the most important selective pressure on the evolution of antipredator mechanism diversity in amphibians (Brodie et al., 1991; Toledo et al., 2007). Anurans display 12 antipredator mechanisms and 28 variations that can be displayed into three phases of defence (i.e., avoid detection, prevent attack, and counterattack) to respond to the risks imposed by predators (Ferreira et al., 2019). For example, mechanisms such as camouflage and immobility can evade detection by visually oriented predators. Display of aposematic colorations, postures, and escape can prevent attacks. Lastly, mechanisms such as cloacal discharge, secretion release, aggression, and distress call can be displayed in counterattacks to apprehension by the predator (Ferreira et al., 2019). In addition, the sequence and intensity of antipredator mechanisms may be displayed according to the degree of stress imposed by a predator. For example, a single individual can display several antipredator mechanisms during an interaction with a predator (Williams et al., 2000; Lourenço-de-Moraes et al., 2016).

The genus of the horned frog *Proceratophrys* Miranda-Ribeiro, 1920 includes 43 species widely distributed in South America (Frost, 2022). They are characterized by the presence of palpebral appendages and cryptic coloration resembling fallen leaves in decomposition (Prado and Pombal, 2008; Toledo and Haddad, 2009), favouring the display of camouflage and postures such as stretching limbs to avoid detection and prevent possible attacks (Ferreira et al., 2019). In the last decades, studies have recorded the antipredator mechanisms such as camouflage, postures, and aggression for some species of *Proceratophrys* (Toledo et al., 2010; 2011; Peixoto et al., 2013; Mângia and Garda, 2015). However, the phylogenetic origin of antipredator mechanisms of *Proceratophrys* genus is still unknown, and a knowledge gap remains with its evolutionary history (Lande and Arnold, 1983; Price and Langen, 1992). Therefore, herein we evaluated the phylogenetic signal of antipredator mechanisms of *Proceratophrys* species. We hypothesized that antipredator mechanisms of *Proceratophrys* species are purely phylogenetic. We also described the antipredator mechanisms diversity and their variations for *P. laticeps* (Izecksohn and Peixoto, 1981), comparing the antipredator mechanisms diversity among congeners.

We extracted the records of *Proceratophrys* species from the global database of antipredator mechanisms (see Ferreira et al., 2019). We complemented this database with our field observations on *P. laticeps*. For this, we conducted fieldwork on November 2018 and November 2019 in the Estação Biologia Marinha Augusto Ruschi (EBMAR; 19°58’09”S, 40°08’37”W), located in the district of Santa Cruz, municipality of Aracruz, Espírito Santo state, south-eastern Brazil. We used focal animal sampling (Altmann, 1974) and induced the antipredator mechanisms under field conditions using only fingers lightly touching the back, fore and hind limbs, and snout of the frogs, simulating predator attacks (Lourenço-de-Moraes et al., 2016).

We followed the classification of antipredator mechanisms proposed by Ferreira et al. (2019). After the field observations, the captured males were sacrificed in 3% lidocaine, fixed in 10% formalin, preserved in alcohol 70%, and deposited at the collection of Museu de Biologia Prof. Mello Leitão (MBML 11562, 11882) from Instituto Nacional da Mata Atlântica, municipality of Santa Teresa, Espírito Santo state, Brazil.

For the phylogenetic analysis, we followed the Amphibia phylogeny of Jetz and Pyron (2018) and reconstructed the ancestral character states through maximum-likelihood estimations under stochastic character mapping analysis (SIMMAP; Bollback, 2006), using 1.000 simulations for discrete characters based on the matrix data of antipredator mechanisms. We used the D statistic for the phylogenetic signal analysis (Fritz and Purvis, 2010) to measure phylogenetic signal for discrete attributes. The statistic adds the differences in attributes among sister clades and compares this sum to one generated by the Brownian movement. To compare phylogenies, this difference in the sums is divided by subtracting the sum of the differences simulated randomly about the sum by Brownian motion using 1.000 simulations. We used the packages “phytools” (Revell, 2012) and “caper” (Orme et al., 2018) through the R software (R Core Team, 2017).

We recorded two calling males of *P. laticeps* (SVL: 66.1 and 66.7 mm) on the partially-submerged leaf-litter of a swampy forest. When we approached, they displayed interrupt calling, and when we hand-manipulated them, both displayed other six antipredator mechanisms and nine variations: camouflage (variation: background matching [Fig. 1A]), immobility, posture (variations: body inflation [Fig. 1B], contraction, gland exposure, stretching limbs, death feigning [Fig. 1C]), escape (variations: hide, jump away), aggression (variation: kick), and distress call.

By adding our field observation on *P. laticeps*, the final dataset comprises 80 records on antipredator mechanisms for 13 species of *Proceratophrys* (Table 1), which represents 33% of the species from the genus. We recorded a total of 11 antipredator mechanisms and 15 variations for species of *Proceratophrys*. The mean of antipredator mechanisms displayed by *Proceratophrys* species was 3.8 (min = 2; max = 7). Camouflage was the most displayed antipredator mechanism (n = 13 species; 100%), followed by posture (n = 12 species; 92%), and escape (n = 8 spe-

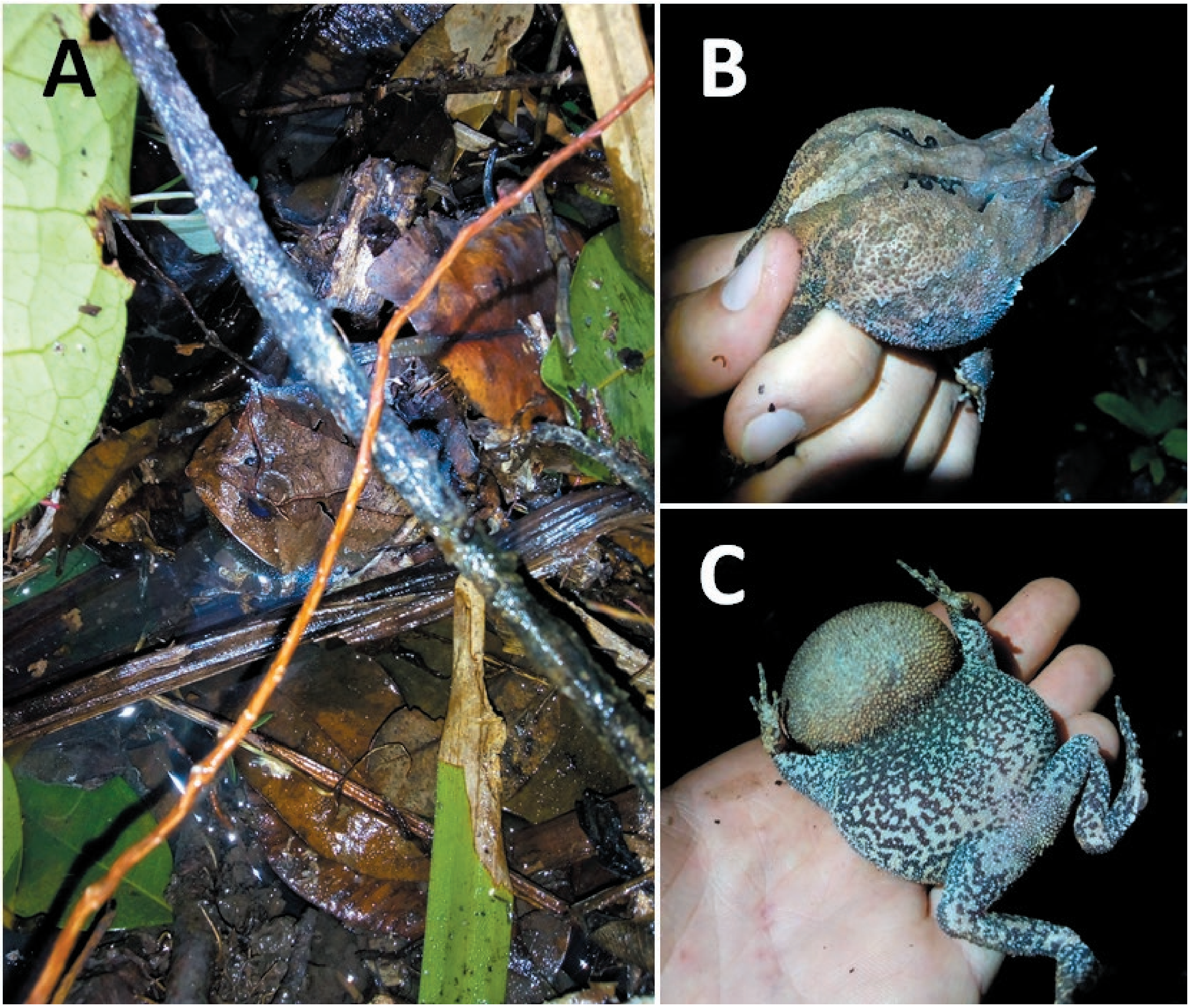

Fig. 1. Antipredator mechanisms displayed by *Proceratophrys laticeps*: A) Camouflage of background matching. B) Posture of body inflation during hand capture. C) Posture of death feigning and body inflation synergistically to distress call.

cies; 62%). Regarding posture, stretching limbs (n = 8 species; 62%), body inflation (n = 7 species; 54%), and death feigning (n = 7 species; 54%) were the most displayed. *Proceratophrys laticeps* (n = 7 mechanisms; 64%) displayed the highest number of antipredator mechanisms, followed by *P. boiei* (n = 6 mechanisms; 55%), and *P. schirchi* (n = 6 mechanisms; 55%). *Proceratophrys schirchi* (n = 12 variations; 80%) displayed the highest number of variations, followed by *P. boiei* (n = 10; 67%).

The mechanisms of camouflage, immobility, interrupt calling, aposematism, aggression, and distress calls (values > 0.60) have high phylogenetic structure values (Table 2). This result indicates that these mechanisms have high similarity in the trees' roots within *Proceratophrys* (Fig. 2). On the other hand, the mechanisms of charge, warning sound, and poisonous secretion have prevalent Brownian origin. This result indicates that these mechanisms can occur randomly at phylogenetic trees' tips.

Proceratophrys species display a wide diversity of antipredator mechanisms to avoid detection, prevent attack, and counter-attack. Despite species of *Proceratophrys* are frequently sampled, only 13 (33%) species have description of antipredator mechanisms. Similarly, only four (40%) species of *Odontophrynus* and 13 (27%) species of *Physalaemus* have been tested but displayed several antipredator mechanisms (n = 11 and 8, respectively) (Ferreira et al., 2019). The lack of data on antipredator mechanisms is generalized across anurans, and thus we reinforce

Table 1. Antipredator mechanisms recorded for *Proceratophrys* species.

Species	Antipredator mechanisms																					Ref
	N	BM	IM	IC	AH	CH	BE	BI	CT	GE	MG	RE	SL	DF	UR	HD	JA	WS	PS	KC	DC	
P. appendiculata	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
P. avelinoi	4	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
P. boiei	18	1	1	0	1	0	0	1	1	1	1	0	1	1	0	0	1	0	0	1	0	3,4,5,6,7
P. brauni	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	8,*
P. cristiceps	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0	9
P. cururu	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	6
P. laticeps	7	1	1	1	0	0	0	1	1	1	0	0	1	1	0	1	1	0	0	1	1	7,*
P. melanopogon	3	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	5,6,10
P. moehringi	3	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	11
P. moratoi	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6,*
P. paviotii	5	1	1	0	0	0	0	1	1	1	1	0	1	1	0	0	1	0	0	1	0	7
P. renalis	2	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	7,12
P. schirchi	6	1	1	0	0	1	1	1	1	1	0	1	1	1	1	0	1	0	0	1	0	7,13
Total	53	13	6	1	2	1	2	7	6	5	3	2	8	7	1	3	6	1	1	4	1	

N= number of individuals tested. Antipredator mechanisms (variations): BM = Camouflage (background matching); IM = Immobility; IC = Interrupt calling; HA = Aposematism (hidden); CH = Charge; Posture (BE = Body elevation; BI = Body inflation; CT = Contraction; GE = Gland exposure; MG = Mouth gape; RE = Rear elevation; SL = Stretching limbs; DF = Death feigning; UR = Unken reflex); Escape (HD = Hide; JA = Jump away); WS = Warning sound; PS = Secretion (Poisonous); KC = Aggression (kick); DC = Distress call. Ref = references: 1 = Sazima, 1978; 2 = Lourenço-de-Moraes and Lourenço-de-Moraes, 2012; 3 = Costa et al., 2009; 4 = Toledo and Zina, 2004; 5 = Toledo et al., 2010; 6 = Toledo et al., 2011; 7 = Ferreira et al., 2019; 8 = Solé, 2003; 9 = Mângia and Garda, 2015; 10 = Moura et al., 2010; 11 = Weygoldt, 1986; 12 = Peixoto et al., 2013; 13 = Mônico et al., 2017; * = Present study.

Table 2. Phylogenetic signal of antipredator mechanisms recorded for species of *Proceratophrys*. Bold values indicate significant differences.

Antipredator mechanisms	Estimated D	Phylogenetic structure	Brownian phylogenetic structure
Aggression	1.753	**0.721**	0.193
Aposematism	8.344	**0.695**	0.130
Camouflage	0.000	**1**	0.000
Charge	-1.691	0.229	**0.527**
Distress call	1.732	**0.841**	0.122
Escape	1.199	**0.548**	0.115
Immobility	2.445	**0.913**	0.071
Interrupt calling	8.119	**0.669**	0.134
Secretion	-3.581	0.136	**0.853**
Posture	0.767	**0.523**	0.278
Warning sound	-4.928	0.243	**0.537**

the need to induce antipredator mechanisms for all individuals from most species collected in the field.

Proceratophrys laticeps displayed high diversity of antipredator mechanisms often in synergy. Anurans displaying different synergistic antipredator mechanisms may be more successful against predators (Toledo et al., 2007), probably because of higher effectiveness in signal transmission to predators as observed for two species of *Gastrotheca* (Lourenço-de-Moraes et al., 2016). Probably, *P. laticeps* displays antipredator mechanisms according to researchers' degree of stress during inductions in the field (see Lourenço-de-Moraes et al., 2016). Despite the high diversity of antipredator mechanisms exhibited, *P. laticeps* differed from the congeners only by interrupt calling. Interrupt calling at predator approach aims to avoid giving predators a cue to the anuran location (Ferreira et al., 2019). Only 10 anuran species have been recorded interrupt calling, thus this homoplastic mechanism have evolved independently in Odontophrynidae (Ferreira et al., 2019). The low number of records of interrupt calling is likely a sampling artifact because most researchers do not take notes on frogs that interrupt the calls when approached in the field.

Camouflage is displayed by all species of *Proceratophrys* studied so far. Camouflage is symplesiomorphic in Anura (Ferreira et al., 2019), and showed high phylogenetic structure in *Proceratophrys*, following a purely phylogenetic model. In fact, camouflage is displayed by most odontophrynids that usually have brown coloration resembling the leaf-litter (Sazima, 1978; Ferreira et al., 2019). Camouflage includes colouring, structural and behavioural adaptations to avoid detection by predators

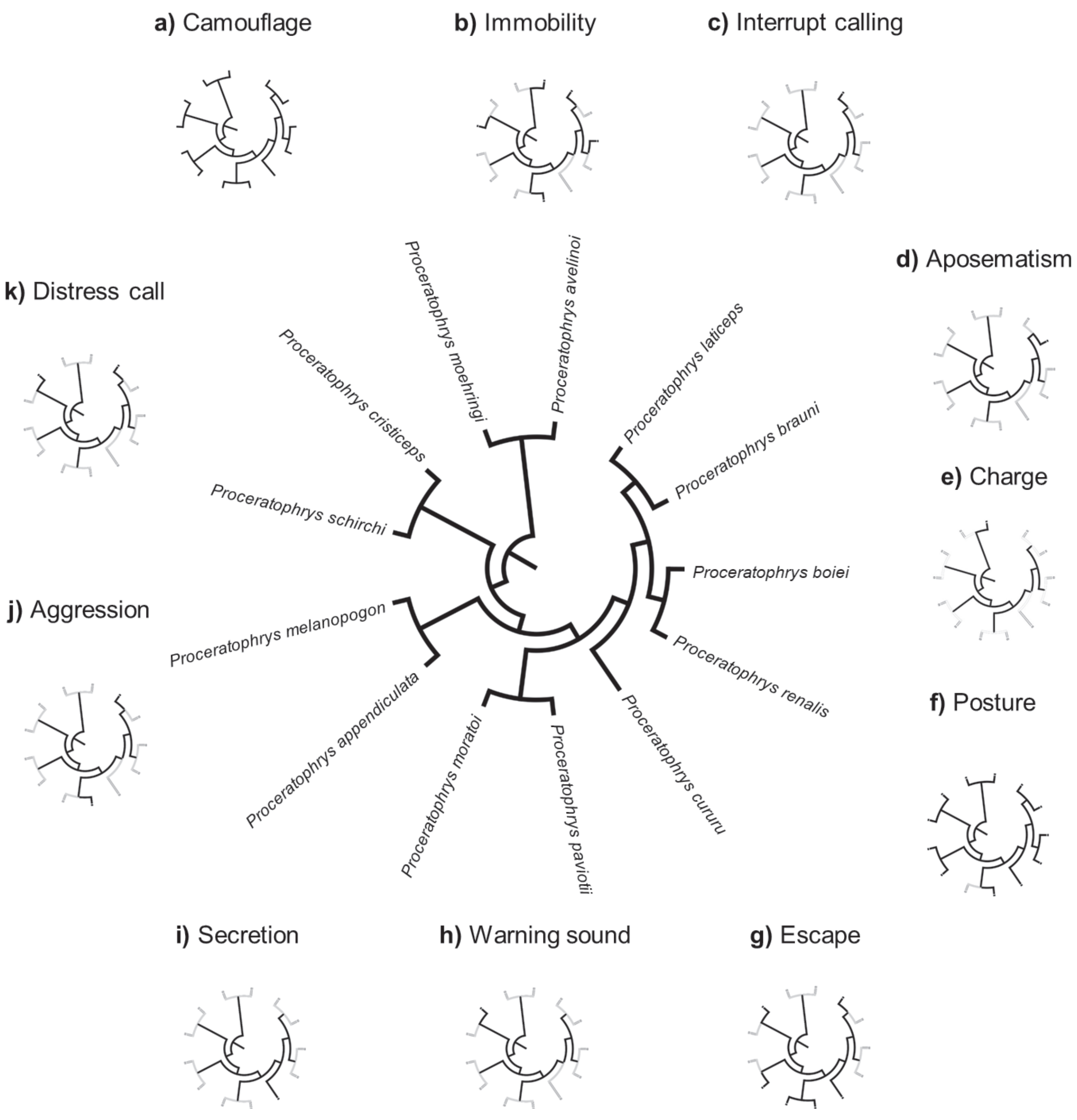

Fig. 2. Reconstruction of ancestral state of 11 antipredator mechanisms displayed by 13 species of *Proceratophrys*. A) Camouflage, B) Immobility, C) Interrupt calling, D) Aposematism, E) Charge, F) Posture, G) Escape, H) Warning sound, I) Secretion, J) Aggression, K) Distress call. Black branches = presence of the mechanism; grey branches = absence of the mechanism.

(Ferreira et al., 2019). In this context, *Proceratophrys* species have morphological adaptations such as supraciliary structures, and a variety of warts and tubercles that likely enhance camouflage (Prado and Pombal, 2008).

After being touched by a predator, *Proceratophrys* species usually display a variety of postures. Posture is symplesiomorphic in *Proceratophrys*, showing high phylogenetic structure, being conserved in the genus and in Anura. Posture was displayed by 12 (30%) species of *Proceratophrys*, and it is the second most displayed antipredator mechanism in the genus. The eight species that displayed stretching limbs may be avoiding detection by visually oriented predators that forage on the leaf-litter (Sazima, 1978). Body inflation can fool the predator regarding anuran body size, becoming difficult to being handled and ingested (Caro, 2014). Death feigning is displayed to resemble a dead organism and generally is displayed after the anuran has jumped away or was handled by a predator (Toledo et al., 2011; Ferreira et al., 2019). Therefore, *Proceratophrys* species likely have success in avoiding predation by displaying postures to intimidate predators, resembling a dead leaf, or making them difficult to be swallowed. We suggest that posture is an effective antipredator mechanism for species of *Proceratophrys* against predators in the leaf-litter.

Our results suggest that there are antipredator mechanisms with strong phylogenetic signal (camouflage, immobility, distress call, aggression, aposematism, and interrupt calling) in *Proceratophrys* and that their evolution is purely phylogenetic. Six antipredator mechanisms displayed by *Proceratophrys* species (i.e., camouflage, immobility, posture, escape, warning sound, and secretion) are plesiomorphic in Anura (Ferreira et al., 2019), explaining the maintenance of these mechanisms in the genus. In contrast, three antipredator mechanisms displayed by *Proceratophrys* species are homoplastic (i.e., interrupt calling, charge, and distress call), having evolved independently.

To conclude, our observations are the first records of antipredator mechanisms for *P. laticeps*, and the first report of interrupt calling in the genus *Proceratophrys*. Also, we showed that several antipredator mechanisms have high phylogenetic signal in this genus. Due to limited sample number of both records of different antipredator mechanism and examined species of the genus, our analysis should be treated as a preliminary overview of possibly more complex phylogenetic scenarios of a number of different mechanisms. We suggest also that further studies on this topic should use standardized induction methods and classification system for antipredator mechanisms (see Ferreira et al., 2019).

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