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Does a Defensive Pseudoautotomy Mechanism Exist in the Subfamily Xenodontinae? A Study of the Genus *Echinanthera*

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Abstract. Pseudoautotomy is presumably a derived character within Lepidosauria and occurs in taxa that have lost the ability to perform autotomy. In general, species capable of employing pseudoautotomy as a defensive strategy against predators present a high frequency of damaged tails in series deposited in herpetological collections. We assessed data from three largely sympatric *Echinanthera* species in the Brazilian Atlantic Rainforest (*E. cephalostriata, E. cyanopleura,* and *E. undulata*) to test previous assumptions that species of *Echinanthera* use their tails defensively. This hypothesis derives from anecdotal observations during fieldwork and is reinforced by the number of specimens presenting tail breakage in scientific collections. In general, the frequency of damaged tails in these species resembles that of others in which pseudoautotomy has been demonstrated. Statistical analyses revealed no differences in tail breakage frequencies between sexes for the analyzed species or between the two geographical groups defined for *E. cyanopleura.* In contrast, we detected a significant difference between snout–vent length and sex regarding pseudoautotomy probability for *E. cyanopleura,* with a positive relationship between tail breakage frequency and snout–vent length.

Keywords. Atlantic Rainforest; Defensive behavior; Echinantherini; Predation; Urotomy.

INTRODUCTION

Urotomy (tail breakage) is a remarkable defensive strategy in lepidosaur reptiles that allows an individual to lose a portion or even its entire tail during predator attacks, increasing the chances of escape (Arnold, 1984; Pough et al., 2004). The best-known kind of urotomy is autotomy, present in tuatura (Rhynchocephalia Günther, 1867) and several lineages of Squamata. The autotomy process involves an intravertebral rupture in specialized tail planes that lead to spontaneous fracture and regeneration whereby the missing osseous tissue is replaced by a cartilaginous shaft (Slowinski and Savage, 1995; Savage and Slowinski, 1996; Pough et al., 2004; Kuhn et al., 2008).

The terminology employed to describe phenomenon requires clarification. Arnold (1984) defined tail autotomy as "a fracture of the tail that occurs in a regular and predictable way at a distinct region of weakness." In doing so, he considered that tail breakage would occur through intravertebral and intervertebral breakage. Arnold (1988) and Cooper and Alfieri (1993) followed the same nomenclature and definition. Mendelson (1992), on the other hand, restricted "tail autotomy" to intravertebral fracture under neural control, designating the term "tail breakage" for intervertebral fractures. However, Slowinski and Savage (1995) noted that some snakes present morphological characteristics that facilitate tail breakage, and that Mendelson's (1992) definition was not sufficiently refined to encompass all anatomical peculiarities. Consequenty, Slowinski and Savage (1995) proposed "urotomy" for all the types of tail breakage, maintaining Mendelson's (1992) restricted use of "autotomy." Additionally, Slowinski and Savage (1995) erected "pseudoautotomy," present in snakes and some lizards (specialized or non-specialized, see below), for intervertebral fractures in different portions of the tail without producing spontaneous rupture or proper regeneration (Etheridge, 1967; Arnold, 1984; Slowinski and Savage, 1995). In this case as the tail rupture is not spontaneous, it depends on external physical

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stimuli (Savage and Slowinski, 1996), and as there is no tissue regeneration, healing is associated with remodeling of the final vertebrae (Arnold, 1984).

Arnold (1984) and Bateman and Fleming (2009) claimed that pseudoautotomy is a derived character within Lepidosauria Haeckel, 1866, occurring in taxa that have lost the ability to perform autotomy. Two mechanisms for this behavior are known in extant snakes. The genera *Enulius* Cope, 1871, *Scaphiodontophis* Taylor and Smith, 1943, and *Urotheca* Bibron, 1843 exhibit specialized pseudoautotomy (a less frequent condition), in which the long, thickened, and fragile tails characteristic of these taxa favor rupture (Savage and Crother, 1989; Savage and Slowinski, 1996). For all other snake species, the term pseudoautotomy refers to non-specialized tail rupture mechanisms (sensu Savage and Slowinski, 1996). This term distinguishes species with moderately long or long tails (< 35% of total length in adult) but lacking anatomical modifications to favor tail rupture (Savage and Slowinski, 1996). Some colubrid genera (e.g., *Coluber* Linnaeus, 1758, *Dendrophidion* Fitzinger, 1843, *Drymobius* Fitzinger, 1843, *Nerodia* Baird and Girard, 1853, and *Thamnophis* Fitzinger, 1843) may present a secondarily induced pseudoautotomy mechanism. When seized by the tail, the snake repeatedly twists its body in a single direction, resulting in tail rupture (Cooper and Alfieri, 1993; Savage and Slowinski, 1996; Marco, 2002; Crnobrnja-Isailović et al., 2016). Finally, Hoogmoed and Ávila-Pires (2011) documented a case of apparently voluntary urotomy in *Dendrophidion dendrophis* (Schlegel, 1837) in which an individual broke its own tail by twisting it firmly against its own body.

Marques and Sazima (2004) raised the hypothesis that *Echinanthera cyanopleura* (Cope, 1885) and *E. undulata* (Wied-Neuwied, 1824) might resort to tail rupture as a defensive strategy on the basis of the number of specimens preserved in scientific collections presenting tail mutilations. Nonetheless, these authors did not discuss specific urotomy mechanisms or test for sex, size, and age effects related to this phenomenon. Gomes (2012), while studying the natural history of *Echinanthera* Cope, 1894 and *Taeniophallus* Cope, 1895, observed an elevated frequency of damaged tails in *Echinanthera* specimens. Zanella and Cechin (2010) and Gomes and Marques (2012) provided brief remarks on tail amputations in preserved *E. cyanopleura* and *E. undulata* individuals, respectively. However, no specific defensive mechanisms involving tail ruptures have been tested or quantitatively explored for xenodontine snakes.

This study assessed data from three largely sympatric *Echinanthera* species (*E. cephalostriata* Di-Bernardo, 1996, *E. cyanopleura,* and *E. undulata;* Fig. 1) in the Brazilian Atlantic Rainforest. Assuming that these tail ruptures reflect evidence of unsuccessful predator attacks, we tested the following hypotheses: (1) the sexual hypothesis, which predicts a higher breakage frequency in males, which presumably present higher mobility during the mating season and are, therefore, more susceptible to predation (Vitt et al., 1974; Bonnet et al., 1999); (2) the size hypothesis, which predicts a higher breakage frequency in larger—and theoretically older—specimens compared to smaller ones, since the former would have probably been exposed to more predation attempts during a proportion-

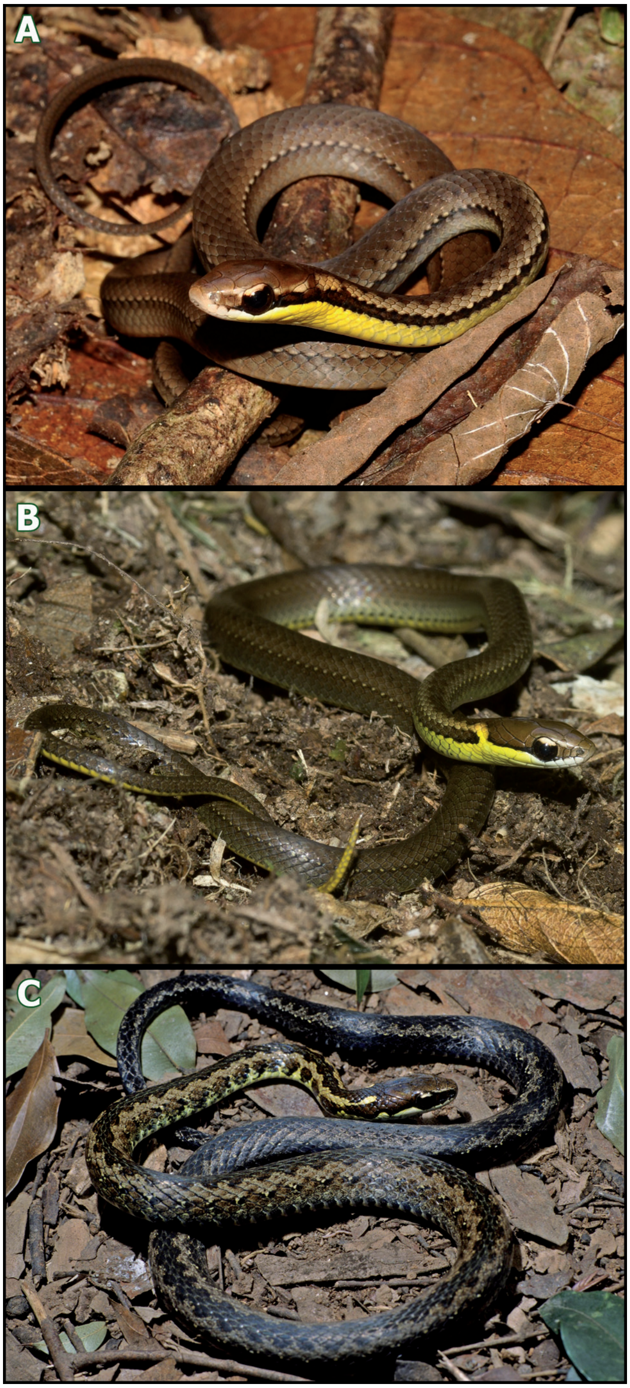

Figure 1. Species analyzed in the present study: **(A)** *Echinanthera cephalostriata* (photo: Renato Gaiga), **(B)** *E. cyanopleura* (photo: Glauco Oliveira), and **(C)** *E. undulata* (photo: Wolfgang Wüster).

ally larger life span than the latter (Mendelson, 1992); (3) the multiple tail break hypothesis, predicting that the remaining portion of damaged tails would be smaller in larger individuals than in smaller ones, considering that larger specimens would suffer several ruptures during their life span (Slowinski and Savage, 1995). Regardless of the last two hypotheses being directly related to age, we also investigated the possibility of geographical variations in the frequency of tail breakage in *E. cyanopleura* since we had access to a more widespread and representative sample.

MATERIALS AND METHODS

Data collection

We examined 80 specimens of *Echinanthera cephalostriata,* 177 *E. cyanopleura,* and 234 *E. undulata* (Appendix), taking the following data: tail condition (intact or healed), snout–vent length (SVL, to the nearest 1 mm), number of subcaudal scales, and sex (determined by midventral incision on the basis of the tail exposing the hemipenis or through gonadal examination). We excluded from our analyses specimens with recent tail breakage (unhealed terminal portion) or partial breakage, considering that recent damages might have resulted from rough handling after preservation. Following the recommendation of Pleguezuelos et al. (2010), we did not consider individuals lacking only the apical scale as specimens with amputated tails.

Data analysis

The Araucaria Moist Forest ecoregion presents several remarkable faunistic endemisms compared to other Atlantic Rainforest areas. These areas harbor endemic mammal species or instances of sympatry of commonly allopatric mammal species (i.e., potential snake predators; Quintela et al., 2014; Cáceres et al., 2016). Thus, for the analysis of geographical variation in *Echinanthera cyanopleura,* we divided our samples into two geographical groups: group 1 comprising highland populations within the Araucaria Moist Forest ecoregion, and group 2 comprising lowland populations within the Alto Paraná Atlantic forests and Serra do Mar coastal forests (sensu Olson et al., 2001). This separation allowed us to evaluate the putative geographic effect related to species overlap with distinct sets of predators, given the wide distribution range of *E. cyanopleura*. We applied a chi-squared independence test in order to evaluate population structure concerning tail breakage for this species.

Given that the sexual hypothesis predicts that differences in tail breakage frequencies between sexes result from behavioral differences during the reproductive season, we restricted sex-associated analyses to sexually mature specimens based on the smallest sizes of reproductively active males and females reported by Zanella and Cechin (2010) for *Echinanthera cyanopleura* (> 288 mm for males and 395 mm for females) and Gomes and Marques (2012) for *E. undulata* (> 276 mm for males and 320 mm for females). Considering the absence of data on the sexual maturation of *E. cephalostriata,* we adopted the same values as for *E. cyanopleura* because of the morphological similarities and putative close phylogenetic relationship between these species (Di-Bernardo, 1996). We also applied a chi-squared test to test this hypothesis.

We tested the size hypothesis using a logistic regression with SVL as the continuous explanatory variable (variable x) under a binary variable response (presence or absence of pseudoautotomy; variable y), following Costa et al. (2014). Regarding the multiple tail break hypothesis, we followed Slowinski and Savage (1995) in applying a linear regression, using the regression of the residual variation concerning the number of subcaudal scales opposed to SVL. If the hypothesis is true, the number of subcaudal scales should decrease with increasing SVL. As SVL and subcaudal scale number are inversely sexually dimorphic in *Echinanthera* (females have greater SVL, whereas males have more subcaudals; see Gomes, 2012), we performed both analyses using sex as the explanatory covariable (ANCOVA).

We tested the multiple tail break hypothesis exclusively for *Echinanthera cephalostriata* and *E. cyanopleura* because the fire at Instituto Butantan (see Franco, 2012) prevented us from obtaining representative data for *E. undulata*. To assess normality and homoscedasticity assumptions, we used the Kolmogorov–Smirnov and Levene tests, respectively. We established alpha < 0.05 for all statistical tests. We performed all statistical analyses in the R software (R Core Team, 2013).

RESULTS

Among the 80 specimens of *Echinanthera cephalostriata* we sampled, 13 (15%) exhibited a healed tail (10.8% of males [*n* = 4]; 22.5% of females [*n* = 9]). We found no juvenile specimens of *E. cephalostriata* with tail mutilations. Among our 177 *E. cyanopleura* specimens (55 males, 80 females, 42 juveniles), 26 (14.7%) presented a healed tail (12.7% of males [*n* = 7]; 23.7% of females [*n* = 19]). Only one juvenile *E. cyanopleura* displayed a mutilated tail. Of the 234 *E. undulata* (85 males, 114 females, and 35 juveniles), 51 (21.8%) exhibited a healed tail (18.8% of males [*n* = 16]; 28.1% of females [*n* = 32]; 8.57% of juveniles [*n* = 3]). Three juveniles of *E. undulata* had mutilated tails.

We detected no differences in tail breakage frequency between sexes for *Echinanthera cephalostriata*

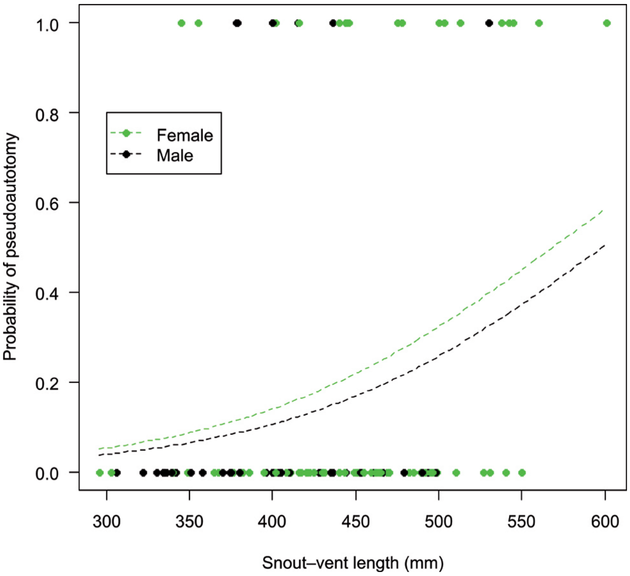

Figure 2. Pseudoautotomy probability in *Echinanthera cyanopleura*. Tail breakage frequency increases in response to snout–vent length increases (R^2 = 0.1068, P = 0.03402).

(χ^2 = 1.1312, P = 0.2875), *E. cyanopleura* (χ^2 = 1.8871, P = 0.1695), or *E. undulata* (χ^2 = 1.5402, P = 0.2146), and no differences in tail breakage frequencies between the two *E. cyanopleura* geographical groups (χ^2 = 0.02959, P = 0.8634). We found, however, a significant difference between SVL and sex with respect to pseudoautotomy probability in *E. cyanopleura* (R^2 = 0.1068, P = 0.03402), with an increased tail breakage frequency associated with higher values of SVL (Fig. 2). In contrast, we detected no differences between SVL and sex for *E. cephalostriata* (R^2 = 0.0964, P = 0.2066) and *E. undulata* (R^2 = 0.0356, P = 0.1822). Finally, regarding the multiple tail break hypothesis, we detected no differences between SVL and sex for *E. cephalostriata* (R^2 = 0.4193, P = 0.1619) and *E. cyanopleura* (R^2 = 0.3397, P = 0.09287).

DISCUSSION

This study demonstrates that the frequency of damaged tails in the assessed species (15% for *Echinanthera cephalostriata,* 14.2% for *E. cyanopleura,* and 21.8% for *E. undulata*) resembles values of other species known to exhibit pseudoautotomy as a defensive mechanism (Bowen, 2004; Gregory and Isaac, 2005; Placyk and Burghardt, 2005; Todd and Wassersug, 2010; Huang et al., 2011; Santos et al., 2011; Costa et al., 2014; but see Broadley, 1987; Mendelson, 1992; Savage and Slowinski, 1996; Aubret et al., 2005; Dourado et al., 2013). Further, field observations describe an *E. cephalostriata* specimen actively rupturing its own tail in an attempt to escape from researchers (Abegg et al., 2018), corroborating predictions by Marques and Sazima (2004). These authors reported a tail break frequency of 33% in *E. cyanopleura* and 12.5% in *E. undulata*. The fact that the latter species presents lower breakage frequency than the former merits attention, considering that tail length is proportionally greater in *E. undulata* ($\bar{x}$ = 47% of the total body size in males, 43% in females) than *E. cyanopleura* ($\bar{x}$ = 34% of the total body size in males, 32% in females; Gomes, 2012).

Assuming that longer tails in certain terrestrial species might not reflect specialized substrate use but rather a defensive mechanism, one should expect higher breakage frequencies in species with longer tails (Martins, 1994; Savage and Slowinski, 1996). However, Marques and Sazima (2004) reported a different result in which tail breakage frequency was lower in *Echinanthera undulata* than *E. cyanopleura*. The contrasting results of the present study (21% for *E. undulata* [n = 234] and 14% for *E. cyanopleura* [n = 174]) might be related to the smaller sample sizes of these authors (*E. cyanopleura* [n = 12]; *E. undulata* [n = 16]), which might have been inadequate to detect the trend for each species.

We found no differences in the pseudoautotomy frequency between the two geographic *Echinanthera cyanopleura* subgroups. Araucaria Moist Forests display particularities with respect to other Atlantic Rainforest formations, including the sympatric occurrence of two South American opossums (*Didelphis albiventris* Lund, 1840 and *D. aurita* Wied-Neuwied, 1826; Didelphidae Gray, 1821) that prey on snakes (Oliveira and Santori, 1999; Cáceres et al., 2016). These species are allopatric throughout most of their distributions, and when in sympatry, they exhibit morphological adaptations and niche displacement (Cáceres et al., 2016). Thus, this sympatry could act as a trigger for higher predation rates of local snake populations by some species. Although we did not test this possibility, the rate of *Echinanthera* specimens with mutilated tails does not provide any evidence supporting geographical effects. Other authors have also reported no inter-population differences in pseudoautotomy frequencies for other snake species (Mendelson, 1992; Costa et al., 2014).

Our results do not support the sexual hypothesis for any of the species we studied. In contrast, females always exhibited higher frequencies of pseudoautotomy, corroborating the findings of other studies (Willis et al., 1982; Fitch, 1999; Placyk and Burghardt, 2005; Pleguezuelos et al., 2010; Santos et al., 2011). Shine et al. (1999) reported a correlation between tail size and reproductive fitness in *Thamnophis sirtalis parietalis* (Say, 1823) whereby males with missing tail tips had a lower reproductive success probability, and, therefore, tail break prevention would help explain the lower frequencies of males with broken tails. Further, Bowen (2004) stated that tail injuries in males might result in damaged hemipenes, limiting survival and fitness. However, Placyk and Burghardt (2005) emphasized that no reliable reports of lethal tail injuries are available. In a different point of view, Fitch

(2003) noted that the higher body mass of females might assist in the tail breaking process in species with higher indices of sexual dimorphism. Indeed, Gomes (2012) detected sexual size dimorphism in species of Echinantherini, which might explain the higher frequency of mutilated tails in females observed in the present study and, additionally, might be indirectly associated with the size hypothesis.

As species of Echinantherini exhibit sexual size dimorphism and higher frequency of damaged tails in females, one could expect a positive correlation for the size hypothesis. However, our results confirmed the size hypothesis only for *Echinanthera cyanopleura,* with a positive correlation between SVL and pseudoautotomy, as also reported for other snake species (Willis et al., 1982; Mendelson, 1992; Gregory and Isaac, 2005; Pleguezuelos et al., 2010; Santos et al., 2011). White et al. (1982) and Costa et al. (2014) found no correlation between these factors for *Nerodia taxispilota* (Holbrook, 1838) and *Drymoluber brazili* (Gomes, 1918) females, and both studies justified their results by insufficient sampling (ca. 60 examined specimens). Even though the same problem might have affected our results for *E. cephalostriata* (*n* = 80), this hypothesis was also not supported for species comprising larger samples (e.g., *E. undulata, n* = 234). Therefore, it is possible that these two species might undergo random tail breakages throughout their lifetimes or that such a pattern might reflect non-mutually exclusive factors such as shifts in the reproductive regime and complex predator–prey interactions.

Although the absence of a relationship between SVL and pseudoautotomy probability in *Echinanthera cephalostriata* and *E. undulata* is surprising, we already expected the low rate of mutilated tails in juveniles (zero *E. cephalostriata* individuals, one *E. cyanopleura,* three *E. undulata*). This is an interesting issue regarding urotomy behavior in lepidosaurs, as the difference between autotomy and pseudoautotomy is not restricted only to the morphological nature of tail breakage, but also to the urotomy frequency between juveniles and adults. LeBlanc et al. (2018) recently demonstrated an ontogenetic difference in vertebral fracture planes in the extinct captorhinid reptiles (a basal lepidosaur clade) as well as in the extant lizard *Iguana iguana* (Linnaeus, 1758). In these groups, juvenile specimens present fracture planes that extend along the entire center of the thinner section of each vertebra, while in adults such planes exhibit some degree of calcification, with consequent lower autotomy frequencies.

Additional causes of differences in pseudoautotomy rates between juveniles and adults remain poorly understood. Costa et al. (2014) speculated that ontogenetic changes in color (when present) might play an important role in the lower juvenile predation rates. In these cases, juveniles usually display a showy coloration (usually conferring disruptive and/or mimetic effects), avoiding predation by primarily visually oriented predators. Alternatively, the low number of specimens with healed tails might reflect lower juvenile survival rates when attacked by predators (Willis et al., 1982). In contrast, Gregory and Isaac (2005) suggested that the behavioral mating of adults entails greater exposure to predators, which would explain differences in tail breaks relative to immature stages. Given that species of Echinantherini do not present obvious ontogenetic changes in coloration during ontogeny, the last two explanations of the lower number of juveniles with mutilated tails seem more plausible, even though the authors suggest unrealistic tests.

Although snakes might be informative models to test the multiple tail break hypothesis (as they do not regenerate portions of their lost tails), evidence of this phenomenon is elusive. This study did not support this hypothesis, which has only documented for *Scaphiodontophis* (Savage and Slowinski, 1996). Along with the other colubrids *Enulius* and *Urotheca, Scaphiodontophis* presents a specialized pseudoautotomy mechanism based on extremely long, thickened, and fragile tails. This is a relatively uncommon condition in snakes that, to the best of our knowledge, has not been documented for any extant lineage within Xenodontinae Bonaparte, 1845 or even Dipsadidae Bonaparte, 1838. However, we must emphasize that the present study represents the first detailed analysis of pseudoautotomy in xenodontines, clearly indicating that this subject remains largely obscure in this snake lineage.

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APPENDIX

Examined specimens. An asterisk (*) indicates damaged tail.

Collection acronyms according to Sabaj-Perez (2016).—IBSP: Instituto Butantan, São Paulo, São Paulo, Brazil; CHUFJF: Universidade Federal de Juiz de Fora, Juiz de Fora, Minas Gerais, Brazil; MCP: Museu de Ciências e Tecnologia, PUC-RS, Porto Alegre, Rio Grande do Sul, Brazil; MHNCI: Museu de História Natural Capão da Imbuia, Curitiba, Paraná, Brazil; MNRJ: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil; MZUSP: Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil; NOPA: Núcleo Regional de Ofiologia de Porto Alegre, Porto Alegre, Rio Grande do Sul, Brazil; UFRGS: Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; UFRRJ: Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil; UPF: Universidade de Passo Fundo, Passo Fundo, Rio Grande do Sul, Brazil; ZUFRJ: Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; ZUEC: Museu de Zoologia da Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; ZUFSM: Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil.

Echinanthera cephalostriata. BRAZIL: **Espírito Santo:** Santa Tereza: MNRJ 785, 786, 787; **Minas Gerais:** Baependi: IBSP 88211*, 88572; Camaducaia: IBSP 29613, 51903, 55169*, 86605; Machado: IBSP 10998; **Paraná:** Antonina: IBSP 30503; Balsa Nova: IBSP 23116; Curitiba: IBSP 4743; Paranavaí: MHNCI 9287*; Piraquara: MHNCI 9015*; **Rio de Janeiro:** Cachoeiras do Macacau: MNRJ 12347, 19288; Duque de Caxias: MNRJ 15420, 15595, 16363, 16122, 16529, 17017, 19377; Friburgo: MNRJ 20365*; Ilha Grande: MNRJ 19183; Mangaratiba: MNRJ 1851, UFRRJ 2470; Marambaia: UFRRJ 250; Paraty: MNRJ 25276; Pedra Branca: MNRJ 1807, 1808; Petrópolis: MNRJ 7744; Rio de Janeiro: MNRJ 7761*, 10978, 15202, 24858; Teresópolis: MCP 5871; **Santa Catarina:** Humboldt: MNRJ 783; Joinville: MNRJ 784; Guaramirim: MNRJ 1857; **São Paulo:** Campos do Jordão: IBSP 9405, 23201, 23610, 45439, 62941, 78873; Capão Bonito: IBSP 27610*; Caieiras: IBSP 68046; Cananéia: 62201; Guarujá: IBSP 22572, 42336, 44127; Iguape: IBSP 32391, 58025; Igaratá: IBSP 70013; Ilha Bela: IBSP 57089*; Itanhaém: IBSP 20799; Itapecirica da Serra: IBSP 40938: Mairiporã: IBSP 72076*; Mogi das Cruzes: IBSP 86059; Ribeirão Grande: MHNCI 12023, 12144*; Ubatuba: IBSP 81698, 81699.

Echinanthera cf. *cephalostriata:* BRAZIL: **Minas Gerais:** Cataguases: MZUFV 2392*, 2393, 2394*; Chácara: CHUFJF 892; **Rio de Janeiro:** Petrópolis: ZUFRJ 562, 1743; Rio de Janeiro: ZUFRJ 6, 554, 869; Teresópolis: ZUFRJ 195, 548, 867; Without locality: ZUFRJ 232; **São Paulo:** Santo André: ZUEC 3441.

Echinanthera cyanopleura (*n* = 174) BRAZIL: **Paraná:** Campina Grande do Sul: MHNCI 9403, 12189; Catanduvas: MHNCI 8427; Curitiba: MHNCI 2233; Dois Vizinhos MHNCI 5948; Fazenda Rio Grande: MHNCI 11019; Santa Helena: MHNCI 3232; General Carneiro: MCP 16173; Guaraniaçu: MHNCI 8088; Mangueirinha: MHNCI 5313, 5314; Manoel Ribas: MHNCI 3454; Mariópolis: MHNCI 10085; Matinhos: MHNCI 9726; Morretes: MHNCI 3002, 9652, 10635, 11618; Pinhão: MCP 7362; Piraquara: MHNCI 3000*, 7537; Porto Grosso: MZUSP 5789; Rio Negro: MHNCI 10518*; Santa Cruz: NOPA 7740*; São João do Triunfo: MHNCI 11849, 11817*, 11814; São José dos Pinhais: MHNCI 817, 2220*, 11744; São Mateus do Sul: MCP 161671, MHNCI 797; Teixeira Soares: MHNCI 8947*, 12984*; Tijucas do Sul: MHNCI 9986; Três Barras do Paraná: MHNCI 8425; União da Vitória: MCP 16169; **Rio Grande do Sul:** Arroio do Tigre: ZUFSM 0091, 2716, 2712, 2358, 2265, 2514; Arvorezinha: MCP 15443*; Bagé NOPA 2749; Bom Jesus: UFRGS 5193; Cachoeira do Sul: MCP 11207; Cambará do Sul: MCP 14415; Canela: MCP 305, NOPA 6446, 13140, 14012; Caxias do Sul: MCP 4648, 12191, 14521*, 14281*; Cerro Branco: MCP 7447; Dois Irmãos: NOPA 10121; Dom Pedro de Alcântara: MCP 4346, 7184, 7899, 8405, 9531, 9532, 9550, 9563, 15552, 15703; Estância Velha: NOPA 7837*; Farroupilha: MCP 1577*; Gramado: MCP 13285, NOPA 12939; Machadinho: NOPA 14310; Maquiné: NOPA 15474*; Morro Reuter: NOPA 14684; Nova Petrópolis: UFRGS 2048, NOPA 13136, MCP 6524, 12189; Osório: NOPA 6557; Passo Fundo: UPF 93*, 654, 693, 695, 715, 803, 804, 862, 867, 878, 881, 890, 893, 902, 913, 919*, 929, 930, 943, 944, 945, 954, 962, 963, 965, 964, 966, 970, 978, 986, 1067, 1069, 1129, 1143, 1172, 1173*, 1096, 1174, 1185, 1175*, 1188, 1117, 1189; Porto Alegre: MCP 2468, 10990, 11794, NOPA 1512, UFRGS 2050; Rosário do Sul: UFRGS 4324, 4326; Salvador do Sul: MCP 12676; Santo Antônio da Patrulha: MCP 1500; Santo Cristo: MCP 11634; São Francisco de Paula: MCP 10996, NOPA 2041, 4619*, 6445; São Leopoldo: NOPA 5901, UFRGS 2051*; São Lourenço: NOPA 7416; Sapucaia do Sul: 8853, 8886; Sarandi: MCP 2532*; Tapes: MCP 14489*; Taquara: MCP 11389; Tenente Portela: NOPA 7201; Torres: NOPA 2747; Viamão: NOPA 2688*; **Santa Catarina:** Anita Garibaldi: NOPA 15374; Bom Jardim da Serra: MZUSP 17230; Brusque: MHNCI 1890; Caçador: MCP 16168; Campo Belo do Sul: NOPA 15610*, UFRGS 4325, 4540; Celso Ramos: NOPA 16551; Fraiburgo: MCP 16172; Porto União: MCP 16170; São Bento do Sul: MZUSP 9448, 9449; São Miguel do Oeste: MCP 15692; **São Paulo:** Boracéia: MZUSP 5699; Cotia: MZUSP 15856; São Miguel Arcanjo: MZUSP 1675; Without locality: NOPA 16339, MHNCI 9287*.

Echinanthera undulata (*n* = 234). BRAZIL: **Minas Gerais:** Poços de Caldas: MZUSP 14055, 14058, MZUSP 14057. **Paraná:** Almirante Tamandaré: MHNCI 6026; Castro: NOPA 7742; Campo Largo: MHNCI 3362; Tijucas do Sul: MHNCI 9980; **Rio de Janeiro:** Magé: MHNCI 3670; **Santa Catarina:** Brusque: MCP 8369; Itapoá: MHNCI 3189*, 7233*, 11891; Joinville: MCP 16751; Santa Luzia: MNRJ 7762*; **São Paulo:** Barueri: IBSP 55757, 55652*, 74074, 16730, 75373, 62670, 1188, 67790, 68820; Bertioga: IBSP 71778, 29453; Birituba Mirim: IBSP 58748; Boracéia: MZUSP 13153; Bragança Paulista: IBSP 74282; Caetetuba: IBSP 4596; Caçapava: IBSP 62393, 4449*; Caieiras: IBSP 55655, 68129*, 74152, 76446, 71013; Cajamar: IBSP 55754, 68100, 76406, 77195, 77194, 70092, 75321*; Calmon Viana: IBSP 23715; Campo Limpo Paulista: IBSP 5037*, 6903*, 7253*, 19161; Campos do Jordão: IBSP 30313, 59470*; Cananéia: IBSP 27418, MZUSP 10251; Canedos: IBSP 9374*; Caraguatatuba: IBSP 13018, 26744, 26748, 26749, 26752, 76780, 26750, 13021, 13018, 13022; Carapicuiba: IBSP 58405, 77294; Caucaia do Alto: IBSP 62557; Córrego Fundo: IBSP 523*; Cotia: IBSP 27134, 28237*, 5531*, 57663, 58250, 58292, 67165, 71264, 72093, 76382, 8246, 74271*, 74272, 75387, 76550-1, 76550-2, 76550-2, 76550-4, 76550-5, MZUSP 12734, 15855; Cubatão: IBSP 22656; Curitibanos: IBSP 1628; Embu das Artes: IBSP 70427, IBSP 29470*; Embu-Guaçu: IBSP 21258; Engenheiro Marsilac: IBSP 34356*; Guararema: IBSP 77211; Guarulhos: IBSP 62934, 76807, 76477, 76478; Horto Florestal: IBSP 72427, 60178; Igaratá: IBSP 63466; Iguape: IBSP 58100, 58142, 76426, 76477; Ilha Comprida: IBSP 52204; Ipanema: IBSP 357, 528; Iporanga: MZUSP 10666, Itaiquara: IBSP 333*; Itapecerica da Serra: IBSP 23390, 59979, 62236, 57741, MCP 4736; Itaquequecetuba: IBSP 9582, 9891*, 10529, 18353, 18354, 18355*, 26569; Itu: IBSP 64232; Jacareí: IBSP 8149, 21183; Jundiaí: IBSP 69888, 69995; Juquiá: IBSP 28421; Mairiporã: IBSP 57589*, 62727, 62458, 65083*, 70159, 71052, 76331, 68247, 77172, 76721; Mogi das Cruzes: MCP 7316, MZUSP 6458*, 6459, 11568*; Nazaré Paulista: IBSP 74279; Osasco: IBSP 62331, 68711; Paraibuna: IBSP 57712*; Paraíso: IBSP 3367; Pedro de Toledo: IBSP 19708; Peruibe: IBSP 7545, 57872; Piedade: IBSP 28561, 28562; Pindamonhangaba: IBSP 14613, 32723; Pinhalzinho: IBSP 62779; Piracicaba: IBSP 788*; 27131; Poá: IBSP 7658, 9338, 9630, 9910, 9970; Porangaba: MZUSP 12900; Registro: IBSP 23638; Riacho Grande: IBSP 60234, 63037*; Ribeirão Grande: IBSP 65533*, 65534*, 65535*; Ribeirão Pires: IBSP 2652*, 16306*, 16305*, 57536*, 57376; São Paulo: IBSP 187*, 739, 1101, 10518, 10026*, 16086, 18175*, 21501, 2168, 24967, 25014, 2644, 2649*, 3249, 5421, 5422, 5661, 5804, 5872, 6036*, 6566, 7019, 9575, 9610, 9933, 10190, 10433, 10238, 10434, 10541, 11412, 11413*, 12467, 12976, 15455*, 18174, 18086*, 18176*, 24966, 26635, 54206, 57746, 58477, 60159, 67940, MCP 16753; São Sebastião: IBSP 60241, 67941, 67942, 64777*; Tremembé: MZUSP 17942; No locality: MCP 1004*, MHNCI 8325*.