

Nesting in the lizard *Phyllopezus pollicaris* (Squamata: Phyllodactylidae) and a phylogenetic perspective on communal nesting in the family

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Abstract

Nesting in the lizard *Phyllopezus pollicaris* (Squamata: Phyllodactylidae) and a phylogenetic perspective on communal nesting in the family. Communal nesting occurs in many reptile species. The hypotheses that explain the evolution of such behaviours are still controversial, but will be better understood as more communal nesting records are described in the literature. We report the findings of two communal nests of *Phyllopezus pollicaris*, including the largest known nest for the species. Our study is the first to provide a communal nesting record for squamate species in a Cerrado core area. We provide nest photographs and detailed neonate measurements and weight. Nests were found during the dry season, in contrast with the reproduction pattern previously described for the species in the Cerrado periphery. We also conducted an extensive literature review seeking all available information on communal nesting information in Phyllodactylidae, and present this information in the context of a phylogenetic tree of phyllodactylid genera. We suggest that studying the correlation between communal nesting evolution and reproductive investment will become a fertile field as more information on lizard nesting becomes available in the literature.

Keywords: Brazil, Cerrado, lizards, nest, phylogeny, reproduction.

Resumo

Ninhadas de *Phyllopezus pollicaris* (Squamata: Phyllodactylidae) e uma perspectiva filogenética de ninhadas comunais para a família. Ninhadas comunais são encontradas em várias espécies de répteis. As hipóteses que explicam a evolução desse comportamento ainda são controversas, mas serão melhor compreendidas à medida que mais registros de ninhadas comunais forem descritos na literatura. Neste estudo, registramos duas ninhadas comunais de *Phyllopezus pollicaris*, incluindo a maior ninhada conhecida para a espécie. Este é o primeiro estudo a registrar ninhadas comunais para

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uma espécie de Squamata em uma região central do Cerrado. Além disso, também apresentamos fotografias das ninhadas, assim como medidas detalhadas e peso dos neonatos. As ninhadas foram encontradas durante a estação seca, em contraste com o padrão reprodutivo previamente descrito para a espécie na periferia do Cerrado. Nós também realizamos uma extensa revisão bibliográfica a respeito de ninhadas comunais na família Phyllodactylidae e apresentamos os resultados no contexto de uma árvore filogenética dos gêneros da família. Finalmente, sugerimos que estudar a correlação entre a evolução de ninhadas comunais e o investimento reprodutivo se tornará um campo de estudo fértil à medida que mais informações sobre ninhadas comunais estiverem disponíveis na literatura científica.

Palavras-chave: Brasil, Cerrado, filogenia, lagartos, ninho, reprodução.

Introduction

Communal nesting, the phenomenon by which different females of one or more species deposit eggs at a shared nest (Noble and Mason 1933), occurs in many squamate species (Graves and Duvall 1995). The evolutionary and ecological processes resulting in this behavior are hypothesized to be related to either environmental constraints or selective advantage (Doody *et al.* 2009). Early attempts to explain squamate communal nesting suggested that this phenomenon was simply a factor of nesting site scarcity (Rand 1967, Vitt 1986). More recent studies, however, advocate that communal nesting evolved through natural selection, since there are potential energetic and reproductive advantages for females that use communal nests. These advantages could be related to less time spent searching and building nests (Graves and Duvall 1995), and to increased offspring performance and/or survivorship (Radder and Shine 2007). Research that used both field collected data and laboratory experiments support the latter hypothesis, and found that communal nesting provided a fitness increase for the involved females (Blouin-Demers *et al.* 2004, Radder and Shine 2007). Nonetheless, the relative prevalence of these alternative processes has not been investigated in a comparative macroevolutionary approach (Doody *et al.* 2009).

Communal nesting has evolved independently several times during the history of squamates

(Doody *et al.* 2009), but appears to be particularly prevalent in geckos (Graves and Duvall 1995, Doody *et al.* 2009). Clutch size is a phylogenetically conserved attribute in geckos (Vitt 1986, Sinervo 1994), and most species produce only one or two eggs at a time (Mesquita *et al.* 2015, 2016a), which is a relatively small number compared to most other lizard families (Mesquita *et al.* 2016b). The repeated evolution of communal nesting in geckos might be a behavioral adaptation in response to this clutch size constraint, as it potentially increases female fitness through better hatchling performance (Blouin-Demers *et al.* 2004, Radder and Shine 2007).

A few Neotropical geckos are known to nest communally, such as *Coleodactylus meridionalis* (Boulenger, 1888) in the Caatinga (Oliveira *et al.* 2015), *Hemidactylus agrius* Vanzolini, 1978 in the Caatinga (Bezerra *et al.* 2011), *Phyllopezus periosus* Rodrigues, 1986 in the Caatinga (Lima *et al.* 2011), and *Gonatodes humeralis* (Guichenot, 1855) in the Amazon (Vitt *et al.* 1997, Oda 2004), among others. To the best of our knowledge, the only known gecko that produces communal nests in the Cerrado, the Brazilian savanna, is *Phyllopezus pollicaris* (Spix, 1825) (Righi *et al.* 2004). Despite the fact that the Cerrado is a biodiversity hotspot (Myers *et al.* 2000) and houses a high proportion of South American lizard diversity (Colli *et al.* 2002, Nogueira *et al.* 2011), natural history information on the reproductive ecology of

Cerrado lizards are still scarce (e.g., Colli 1991, Wiederhecker *et al.* 2002, Colli *et al.* 2003).

The lizard *Phylllopezus pollicaris* is distributed across the dry-diagonal biomes of South America (Caatinga, Cerrado, and Chaco) (Werneck and Colli 2006). Although there are no recent taxonomic changes related to the status of *P. pollicaris*, it is certainly a species complex composed of many cryptic lineages (Gamble *et al.* 2012, Werneck *et al.* 2012). In terms of habitat use, *P. pollicaris* is mostly found on rock outcrops (Werneck *et al.* 2009), either granite (Vitt 1986) or sandstone (Recoder *et al.* 2012), where they forage and lay their eggs (Righi *et al.* 2004, Recoder *et al.* 2012). Individuals of this species are surface active during the night and usually found within rock crevices during the day (Recoder *et al.* 2012). According to literature records, *P. pollicaris* is only known to produce two eggs (Vitt 1986, Ávila and Cunha-Avellar 2005, Recoder *et al.* 2012, Righi *et al.* 2012).

Vitt (1986) was the first author to suggest that *Phylllopezus pollicaris* will nest communally, and found nests with a maximum number of six eggs (probably produced by three females) in the Caatinga biome. Ávila and Cunha-Avellar (2005) recorded a similar instance (single nest with six eggs) in seasonally-dry forests in western Brazil. Finally, Righi *et al.* (2004) found five communal nests with two to 10 eggs (i.e., produced by up to five females) in a Cerrado peripheral area, southeastern Brazil. The only available information on neonates of this species is average snout vent length and weight, which were based on a limited number of individuals (Vitt 1986), and snout vent length and tail length of two individuals (Gomides and Garcia 2014). Herein, we report the largest communal nest found for *P. pollicaris*, provide the first record of squamate communal nesting in a Cerrado core area, and visual records of such nests in the biome. We also provide detailed neonate measurements and weight (Table 1, Appendix I). Finally, we present this information with a communal nesting phylogenetic perspective for the family Phyllodactylidae.

Table 1. Descriptive statistics of body measurements (mm) and mass (g) of *Phylllopezus pollicaris* neonates ($N = 22$) from two communal nests in the Cerrado biome.

Neonates measurements	Mean \pm SD
Mass	0.88 \pm 0.06
Snout vent length	32.53 \pm 1.12
Tail length	34.19 \pm 1.53
Body width	6.65 \pm 0.65
Body height	4.57 \pm 0.48
Head width	6.90 \pm 0.40
Head height	3.82 \pm 0.30
Head length	9.80 \pm 0.58
Anterior limb length	9.91 \pm 0.70
Posterior limb length	13.62 \pm 0.71

Materials and Methods

We searched for *Phylllopezus pollicaris* nests for three consecutive days (18–20 May 2013) at Parque Nacional Chapada dos Veadeiros (Alto Paraíso de Goiás, Goiás state, Brazil), a large protected area at the core of the Cerrado biome. Searches were conducted in a ‘cerrado rupestre’ area (14°9'47.26" S, 47°37'9.46" W), which consists of typical cerrado (savanna) vegetation growing amidst sandstone rock outcrops (Figure 1A, B). Sandstone rocks are found in many different sizes, and it is common for lizards to hide and nest under rocks laying on top of larger rocks (Recoder *et al.* 2012). Hence, we spent ~8 hours per day searching for eggs in rock crevices, and also lifting smaller rocks, since nests could potentially be found under such rocks. When found, all eggs from a nest were collected, taken to the laboratory to hatch, and kept at room temperature (~21°C) in separate closed plastic containers (lids had holes to allow for gas exchange). Since there was no soft substrate in

the rocks where eggs were collected (e.g., litter or sand), they were kept in exfoliated vermiculite.

Neonates were killed immediately after hatching using a 2% lidocaine hydrochloride injection. Body measurements of the neonates were taken to the nearest 0.01 mm using a digital caliper (Mitutoyo®), and weighing to the nearest 0.01 g was performed using a digital scale (A&D Company®). To allow for future genetic investigations, we also extracted the liver from all lizards after measurements were performed. Livers were preserved in 99% ethanol, and lizards were fixed in 10% formalin. All lizards and tissue samples were deposited at Coleção Herpetológica da Universidade de Brasília (CHUNB) (Appendix I).

To place our results in a broader evolutionary perspective within the Phyllodactylidae, we conducted a literature review of published information on communal nesting for this family. We sought published papers and notes on nests of all synonyms of the 135 currently described species of Phyllodactylidae (Uetz 2016). Since the absence of communal nesting behavior is virtually impossible to determine, it becomes impractical to reconstruct the evolution of this trait in a phylogenetic context using only the relatively few cases where communal nesting is actually present. Hence, following the approach of Doody *et al.* (2009), we plotted the available information in a phylogenetic tree of all currently recognized phyllodactylid genera, in order to visualize the macroevolutionary patterns of this behavior. We used the most recent Squamate phylogenetic estimate (Tonini *et al.* 2016), and pruned the tree so it would only depict the relationships among phyllodactylid genera, using the package *ape* (Paradis *et al.* 2004) in R version 3.3.1 (R Core Team 2016).

Results

We found two *Phyllopezus pollicaris* communal nests, one containing 25 eggs (Figure 1C, D), hereafter Nest 1, and another containing six eggs (Figure 1E), Nest 2. Both nests were

found on 19 May 2013 under stacked rocks. All eggs were hard shelled and oviposition occurred directly on the rocks. From Nest 1, 80% of the eggs hatched ($N = 20$), and from Nest 2 50% ($N = 3$). Incubation time since field collection ranged from 3 to 112 days (mean \pm SD: 30 ± 32.5 days; Appendix I). Neonates measurement and mass descriptive statistics can be found in Table 1.

In our literature review, out of the 135 currently described phyllodactylid species, we found 21 species for which communal nesting evidence is available (Table 2), distributed among seven out of the 10 phyllodactylid genera (Figure 2, Appendix II).

Discussion

Females of *Phyllopezus pollicaris* may take up to three months to produce eggs when reproduction season starts (i.e., time between first vitellogenic follicles and first gravid females are found) (Righi *et al.* 2012), and it took between three and 112 days for our captured eggs to hatch in captivity. Hence, it is not possible, at this stage, to evaluate whether at least some ovipositions in *P. pollicaris* communal nests were produced by the same females. We believe that future genetic investigations using the collected tissue samples, and possibly other nests, might clarify this issue.

The uneven number of eggs in Nest 1 is somewhat surprising, because *Phyllopezus pollicaris* is believed to always produce two eggs (Vitt 1986, Righi *et al.* 2012). This finding might be explained by egg predation, or simply by the female's choice to lay one egg at a separate location, since no empty shells were found at Nest 1. Although very unlikely, the fact that we found the same incubation time for three eggs in two distinct cases (Appendix I), and the arrangement of two rows of three eggs each in Nest 2 (Figure 1E) might suggest that *P. pollicaris* could produce up to three eggs in our study site. We visually inspected all Chapada dos Veadeiros *P. pollicaris* specimens deposited



Figure 1. *Phyllopezus pollicaris* communal nests. (A–B) The ‘cerrado rupestre’ habitat at Parque Nacional da Chapada dos Veadeiros. Nest 1 with 25 eggs, (C) 22 at the bottom rock and (D) three stuck at the top rock. (E) Nest 2 with six eggs disposed in two rows of three eggs each. Photographs of nests were taken after the removal of the top rocks during the searches.

at CHUNB ($N = 22$) but, unfortunately, there were no pregnant females that could shed light on this question. This hypothesis might be tested when more *P. pollicaris* communal nests are found, and specimens are collected during the reproductive season at Chapada dos Veadeiros.

Vitt (1986) suggested that communal nesting by geckos in arid areas might simply be a factor of the limited amount of nesting sites. However, we spent ~ 24 working hours checking many

possibly suitable nesting sites and found only two nests. Since nesting sites appear to be abundant in the area, and considering that one nest contained such a large number of eggs (25), we suggest that Vitt’s assumption might not be true for *P. pollicaris* living in the Cerrado. The alternative explanation, that communal nesting might increase *P. pollicaris* female fitness because of egg insulation, predation abatement, increased hatchling quality, or other mechanisms,

Table 2. Phyllodactylidae species known to lay eggs communally, and reference list from where communal nesting information was obtained.

Species	References for communal nesting
<i>Gymnodactylus amarali</i> Barbour, 1925	(Vitt pers. comm. in Doody <i>et al.</i> 2009)
<i>Gymnodactylus darwini</i> (Gray, 1845)	(Cassinio and Rodrigues 20110)
<i>Gymnodactylus geckoides</i> Spix, 1825	(Vitt pers. comm. in Doody <i>et al.</i> 2009)
<i>Homonota borellii</i> (Peracca, 1897)	(Godoy and Pincheira-Donoso 2009)
<i>Homonota uruguayensis</i> (Vaz-Ferreira & Sierra de Soriano, 1961)	(Gudynas 1986)
<i>Phyllodactylus galapagensis</i> Peters, 1869	(Kushlan 1981)
<i>Phyllodactylus interandinus</i> Dixon & Huey, 1970	(Dixon and Huey 1970)
<i>Phyllodactylus kofordi</i> Dixon & Huey, 1970	(Dixon and Huey 1970)
<i>Phyllodactylus leoni</i> Torres-Carvajal, Carvajal-Campos Barnes, Nicholls and Pozo-Andrade, 2013	(Torres-Carvajal <i>et al.</i> 2013)
<i>Phyllodactylus reissii</i> Peters, 1862	(Dixon and Huey 1970)
<i>Phyllodactylus transversalis</i> Huey, 1975	(López-Victoria <i>et al.</i> 2013)
<i>Phyllodactylus wishingi</i> Kerster & Smith, 1955	(Graves and Duvall 1995)
<i>Phyllopezus periosus</i> Rodrigues, 1986	(Lima <i>et al.</i> 2011)
<i>Phyllopezus pollicaris</i> (Spix, 1825)	(Vitt 1986, Righi <i>et al.</i> 2004, Ávila and Cunha-Avellar 2005, Comides and Garcia 2014, this study)
<i>Phyodactylus guttatus</i> Heyden, 1827	(Disi <i>et al.</i> 2001)
<i>Phyodactylus hasselquistii</i> (Donndorff, 1798)	(Werner 1965, Werner 1972, Werner 1986, Roobol <i>et al.</i> 2002)
<i>Phyodactylus oudrii</i> Lataste, 1880	(García-Márquez <i>et al.</i> 1996)
<i>Tarentola americana</i> (Gray, 1831)	(Schwartz 1968, Novo 1985, Schwartz and Henderson 1991)
<i>Tarentola crombiei</i> Diaz & Hedges, 2008	(Diaz and Hedges 2008, Alfonso <i>et al.</i> 2012)
<i>Tarentola mauritanica</i> (Linnaeus, 1758)	(Bons 1959) (Petzold 1982, González de la Vega 1988)
<i>Thecadactylus rapicauda</i> (Houttuyn, 1782)	(Vitt <i>et al.</i> 1997)

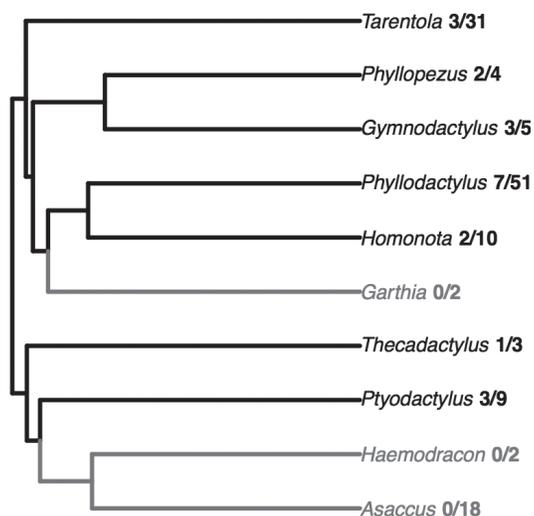


Figure 2. Phylogenetic relationships among currently recognized genera of Phyllodactylidae (number of species known to nest communally/number of species in the genus). Tree adapted from Tonini *et al.* (2016). Genera known to lay eggs communally are in black, and genera for which no evidence of communal nesting is available are in gray.

should be further studied to test this suggestion (Doody *et al.* 2009).

Interestingly, *Phyllopezus pollicaris* reproduces throughout the year in the Caatinga (Vitt 1986), but only between August and December in the Cerrado (Righi *et al.* 2012), during the end of the dry season and through part of the wet season (Eiten 1972). The same pattern is true for two other phyllodactylid sister species: *Gymnodactylus geckoides* Spix, 1825, which reproduces continuously in the Caatinga, and *G. amarali* Barbour, 1925 which reproduces during the Cerrado dry season (Colli *et al.* 2003). This pattern is probably related to the unpredictability of Caatinga's climate, leading lizards to constantly invest in reproduction (Colli 1991, Mesquita *et al.* 2016a), and also suggests that large Phyllodactylidae communal nests will be mostly found in the Cerrado

biome, where reproduction is concentrated in a few months. On the other hand, we found nests at the start of the dry season, outside the estimated reproduction time for *P. pollicaris* in another Cerrado location (Diamantina, Minas Gerais state) at the southeastern border of the biome (Righi *et al.* 2012). It is beyond the scope of this manuscript to infer reproduction seasonality aspects of *P. pollicaris*, but such large difference might be related to climatic differences between both localities, or to the cryptic lineages within the species (Werneck *et al.* 2012). Coincidentally, reproduction of other phyllodactylid species, *G. amarali*, is also concentrated during the dry season in Cerrado core areas (Colli *et al.* 2003). The same is not true for other lizard species such as *Ameiva ameiva* (Linnaeus, 1758) (Colli 1991) and *Tropidurus torquatus* (Wied-Neuwied, 1820) (Wiederhecker *et al.* 2002) which reproduce during the wet season at the core of Cerrado. Hence, there is also the possibility that differences between the peripheral and core Cerrado climate influences this shift in the reproduction patterns of phyllodactylid species (Furley 1999, Souza *et al.* 2015).

Communal nests may provide thermal insulation for eggs, which could in turn lead to increased growth of embryos and a fitness advantage for females (Blouin-Demers *et al.* 2004). This is apparently true in temperate regions, but could be an important selective pressure in the cold nights of the Cerrado dry season. If this hypothesis is true, we predict that: (1) within populations, neonates from nests with fewer eggs would be smaller than neonates from nests with more eggs; and (2) between populations, we would find nests with more eggs in colder regions as opposed to nests with fewer eggs in warmer regions. We could not detect a significant difference in body sizes of neonates from the two nests sampled in this study (results not shown), contradicting our first prediction. On the other hand, we registered the largest *P. pollicaris* communal nest to date, as opposed to smaller nests found both in the Caatinga (Vitt

1986, Gomides and Garcia 2014), which presents warmer climate, and in the Cerrado during the wet season (Righi *et al.* 2012), which is usually warmer than the dry season. Average snout vent length of *P. pollicaris* neonates in this study (32.53 ± 1.12 mm) was similar to the measurements obtained by Vitt (1986) in a Caatinga area (31.0 ± 0.55 mm). However, a sample of two laboratory hatched *P. pollicaris* also from the Caatinga were considerably smaller (24.82 ± 0.04 mm) (Gomides and Garcia 2014). Investigating the possible fitness advantage of communal nesting on neonate size would require a comprehensive database of hatchlings size and adult females among populations of *P. pollicaris* (and closely related species), and our complete set of measurements will be a valuable source of information for future comparative studies. This hypothesis should also be explored in an integrative approach, by testing the effects of temperature on embryo development in the laboratory, and by assessing nests microclimate in the field.

Alternatively, communal nesting might have little or no effect on neonate size in Phyllodactylidae, since the rigid eggshell acts as an important constraint in this trait (Pike *et al.* 2011). In lineages with fixed clutch size, allocating resources for multiple clutches per reproductive season is a common strategy to increase reproductive success (Meiri *et al.* 2012, 2015). Genetic analysis of the samples collected in this study will provide a rare opportunity to detect if females are producing multiple clutches and using the same nesting site. Nevertheless, considering the constraints in the reproductive biology of phyllodactylids, communal nesting could represent a significant fitness advantage for *P. pollicaris* individuals. Some of the adaptive hypotheses that might explain this phenomenon in the species include reduction in eggs predation, reduction in energetic costs to find nesting sites for females, and increasing survival of embryos and hatchlings (Graves and Duvall 1995, Doody *et al.* 2009).

The relatively high proportion of species known to nest communally in Phyllodactylidae (Figure 2) shows that such behavior is particularly prevalent in the family. Apart from the species-rich genus *Phyllodactylus*, all genera have between 1 and 3 species known to lay eggs communally (Figure 2, Appendix II). The phylogenetic distribution of communal nesting in phyllodactylid genera strongly suggests that this is an ancient behavior, ancestral in the family. This finding is not particularly surprising, given that communal nesting behavior is known for members of most currently recognized Gekkota families (Doody *et al.* 2009). Communal nesting has not been recorded in *Garthia*, *Asaccus* or *Haemodracon* species, which could suggest that such behavior was lost at least twice during the evolution of the family (Figure 2). However, there is not much ecological information on the few species in these genera (Marquet *et al.* 1990, Razzetti *et al.* 2011), and future detailed studies may unearth this behavior in these genera.

Communal nesting is a recurrent feature of gecko evolution (Graves and Duvall 1995, Doody *et al.* 2009) and, notably, species of the family Phyllodactylidae display some of the highest levels of investment per progeny of all lizard families (Mesquita *et al.* 2016b). Therefore, the possible fitness gain by communal nesting might be related to the high reproductive investment in relation to the low female longevity found in *Phyllopezus* species (Mesquita *et al.* 2016b). The same relationship might explain why this behavior is present in so many phyllodactylid species (Figure 2). Although, at this stage, this should be interpreted only as a rudimentary association, studying the correlation between communal nesting evolution and reproductive investment should become a fertile field as more information on lizard nesting becomes available in the literature.

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Appendix 1. Body measurements (mm), mass (g), and incubation time since field collection (days) of *Phyllomedusa* pollicaris neonates. One neonate was not measured (CHUNB-72555; incubation = 7 days), and is not included in this table; two other neonates (CHUNB-72588 and 72589) could not have their hatching day recorded (hatching occurred between July 10th and 31st 2013) and were not included in the average incubation time calculation (30.0 ± 32.5 days).

Museum voucher	Mass	Snout vent length	Tail length	Body width	Body height	Head width	Head height	Head length	Anterior limb length	Posterior limb length	Communal nest (# eggs in nest)	Incubation since collection
CHUNB-72547	0.90	32.61	33.96	6.91	5.02	7.28	3.69	10.24	10.94	14.16	Nest 1 (25)	3
CHUNB-72548	0.90	31.35	33.80	7.42	5.31	6.83	3.43	9.89	9.61	13.93	Nest 1 (25)	3
CHUNB-72549	0.90	31.78	34.03	7.16	3.87	7.03	4.16	9.54	9.41	12.57	Nest 1 (25)	3
CHUNB-72551	0.90	33.84	36.18	7.37	4.35	6.75	3.43	10.23	10.17	13.53	Nest 1 (25)	4
CHUNB-72552	0.80	32.86	35.65	7.00	4.15	6.83	3.56	10.14	9.24	13.89	Nest 1 (25)	4
CHUNB-72553	0.90	33.48	34.10	7.14	4.86	6.77	3.95	10.65	9.80	14.32	Nest 1 (25)	7
CHUNB-72554	0.90	32.30	32.80	7.69	4.18	6.99	3.56	9.68	9.13	12.32	Nest 1 (25)	7
CHUNB-72561	0.94	34.17	33.91	7.04	4.86	6.76	3.78	9.66	9.91	14.38	Nest 1 (25)	15
CHUNB-72562	0.96	30.08	35.65	6.70	5.10	6.77	3.51	9.98	9.41	12.42	Nest 1 (25)	15
CHUNB-72563	0.96	32.14	35.99	7.35	5.15	6.66	3.78	10.27	10.60	14.15	Nest 1 (25)	15
CHUNB-72580	0.92	33.46	35.82	6.70	4.51	7.55	3.47	9.83	10.27	14.31	Nest 1 (25)	29
CHUNB-72581	0.91	33.17	32.44	6.11	4.17	7.08	3.95	9.87	10.93	14.16	Nest 1 (25)	29
CHUNB-72582	0.85	32.24	33.82	6.20	4.53	6.10	4.17	9.53	10.21	13.82	Nest 1 (25)	31
CHUNB-72583	0.95	32.21	34.82	6.81	4.03	7.38	4.32	9.55	9.30	12.60	Nest 1 (25)	31
CHUNB-72585	0.91	33.40	35.88	5.72	4.03	6.65	3.70	9.55	9.26	13.57	Nest 1 (25)	32
CHUNB-72586	0.80	31.43	31.45	5.62	4.10	6.51	3.88	7.89	9.35	13.55	Nest 1 (25)	36
CHUNB-72588	0.75	34.35	34.44	5.71	4.75	7.10	4.54	10.48	10.99	14.42	Nest 2 (6)	52 to 72
CHUNB-72589	0.80	33.98	35.59	6.04	3.83	7.29	3.97	10.61	11.02	14.06	Nest 2 (6)	52 to 72
CHUNB-72590	0.83	32.25	33.41	7.00	4.83	7.60	3.92	9.83	10.38	12.91	Nest 1 (25)	74
CHUNB-72591	0.84	30.95	34.89	6.96	4.51	6.60	3.94	9.46	8.81	14.27	Nest 1 (25)	74
CHUNB-72599	0.84	32.12	33.23	5.62	5.06	6.07	3.44	9.31	9.04	12.65	Nest 2 (6)	99
CHUNB-72601	0.79	31.49	30.36	6.08	5.35	7.09	3.86	9.45	10.26	13.60	Nest 1 (25)	112

Appendix II. Phylogenetic tree depicting all currently recognized species in the family Phyllodactylidae, extracted from Tonini et al. (2016). Species known to lay eggs communally are in black, and species for which no evidence of communal nesting is available are in gray.

